A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With four plates

Subgenus VII. **Botryanthus** Webster, Jour. Arnold Arb. 37: 345. 1956.

Trees or shrubs with non-phyllanthoid branching, the leaves on the main axes not reduced to scales, ultimate axes not regularly deciduous. Monoecious; flowers borne in thyrses or axillary clusters. Male flower: calyx-lobes 5 or 6; disk-segments 5 or 6, often massive; stamens 3, filaments connate, anthers dehiscing horizontally or obliquely; pollen grains globose, areolate. Female flower: calyx-lobes 5 or 6; disk cupuliform; ovary of 3 carpels, smooth; styles erect or spreading, usually connate (at least basally) into a column, the tips entire to bifid. Fruit capsular, sometimes very large; seeds trigonous, essentially smooth.

Subgenus *Botryanthus* is an entirely Neotropical group which includes possibly 35 species, most of these occurring in Central and South America. In addition to the dubious sect. *Diplocicca* from Brazil (based on *P. octomerus* Muell. Arg.), other South American sections may eventually be defined; but the majority of the species in the subgenus (including all the West Indian ones) clearly are referable to sect. *Elutanthos*.

From the phylogenetic point of view subg. *Botryanthus* is of especial interest because it is closely related to subg. *Xylophylla*. Its areolate pollen grains are essentially identical to those of the latter subgenus and, since its branching is non-phyllanthoid (and hence presumably unspecialized), subg. *Botryanthus* might logically be considered the ancestral group. The reduction series in inflorescence within sect. *Elutanthos* (which can be traced from the elaborate "panicle" of *P. grandifolius* to the axillary flowers of *P. nutans* ssp. *grisebachianus*) could furthermore be cited in support of such a supposition. On the other hand, it must be noted that in many ways *P. grandifolius* is a very specialized plant, for it has capsules and seeds extraordinarily large in the genus, and its male flowers with three connate stamens give no indication of primitiveness. A rather convincing argument could be put forth to read the phylogeny in precisely the opposite direction, and to assume that subg. *Botryanthus* has evolved from some group within subg. *Xylophylla* (such as sect. *Asterandra*) by a regression from phyllanthoid to non-phyllanthoid branching. Such a hypothesis would involve the assumption that a great increase in leaf and fruit size (such as occurs in *P. grandifolius*) would place a selective advantage on any reversion from deciduous to permanent reproductive axes. At present a decision for either of the alternative hypotheses can-

* Continued from volume XXXVIII, p. 373.

not be made, but with the accumulation of additional evidence (particularly from cytology) it should be possible to do so.

Sect. 15. **Elutanthos** Croiz. Jour. Wash. Acad. Sci. 33: 12. 1943.

Shrubs or trees with unspecialized ramification, leaves distichous on persistent axes. Monoecious; flowers in cymules in the axils of foliage leaves or of bracts (the inflorescence then thyrsoid), or sometimes solitary. Male flower: calyx-lobes 6; disk-segments 6, often massive; stamens usually 3, filaments completely united into a column; anthers dehiscing more or less horizontally (or deflexed); pollen grains globose, areolate, the areoles usually polybrochate. Female flower: calyx-lobes 6; disk patelliform; styles erect, connate at least below, entire to bifid. Capsule obscurely rugulose; seeds smooth.

TYPE SPECIES: *Phyllanthus glaucescens* H.B.K. [= *P. grandifolius* L.].

As established by Croizat, sect. *Elutanthos* included seven species of Central and South America; but there are undoubtedly a number of others which are to be referred here, including the following six species from the West Indies. The West Indian plants differ from the mainland *P. grandifolius* and its allies in their smaller capsules and less elaborate inflorescence, but the similarities are so striking that there is obviously a close affinity.

The combination of an indefinite branching pattern and usually raceme-like inflorescence distinguishes the species of sect. *Elutanthos* from all other woody West Indian species. However, the expression of inflorescence is quite variable and the typical thyrses are not developed in *P. nutans* ssp. *grisebachianus* and some forms of *P. nutans* ssp. *nutans*. Where the raceme-like thyrses occur, they often appear to be terminal, but close inspection will show that each thyrse does not represent a continuation of the branch axis but is rather inserted just below the abortive tip of the axis; often an additional thyrse is produced at one or more additional nodes below. In addition, cymules may also occur in the axils of foliage leaves; in such cases, these axillary cymules tend to be male and the ones in the "racemes" female. The homology between the more or less naked thyrses and the leafy branch-ends is as ill-defined as that between branch-orders, for the degree of distinctiveness of thyrse development is at least partially dependent on the vigor of the branches. Sometimes there may be long "leader" shoots which bear short thyrsiferous branchlets in distichous order, but in other instances the thyrsiferous branchlets may themselves be of the penultimate order and produce additional leafy axes as well as "racemes" of flowers.

Ecologically the West Indian representatives of sect. *Elutanthos* are characterized by a xerophytic tendency, most of the species appearing to grow in open scrub formations at low altitudes. The widespread *P. nutans*, however, occurs in a considerable variety of habitats, including some of the wettest rain forest in Jamaica.

KEY TO THE SPECIES

1. Calyx-lobes of male flowers less than 1.5 mm. long; capsules trigonous; plants of the southern Caribbean.
   2. Styles subentire (truncate-emarginate), completely erect and connivent (with no reflexed portions); disk of female flower extremely massive; plants completely glabrous; Curaçao. ..... 43. *P. botryanthus*
   2. Styles with bifid sharply reflexed tips; disk of female flower tenuous; branchlets and inflorescence axes hirsutulous; Barbados. ..... 44. *P. anderssonii*

1. Calyx-lobes of male flowers over 1.5 mm. long; capsules rounded; plants of the northern Caribbean.
   2. Staminal column with 3 apiculae alternating with the anthers; leaf-blades densely hirsutulous beneath, sparsely hirsutulous above; style-tips entire or merely emarginate; Haiti. ..... 47. *P. urbanianus*
   2. Staminal column without apiculae; leaf-blades glabrous or sparsely hirsutulous beneath, glabrous above; styles definitely bifid.
      3. Leaf-blades rigidly coriaceous, the main veins distinctly sunken above; stipules indurate, dark and shiny, colored as the branch; Cuba. ..... 46. *P. pachystylus*
      3. Leaf-blades chartaceous, the veins not sunken above; stipules not indurate; Jamaica and Cuba. ..... 45. *P. nutans*

43. **Phyllanthus botryanthus** Muell. Arg. in DC. Prodr. **15**(2): 323 1866. (PLATE XXIV, *figs.* A–B).

Diasperus botryanthus (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 598. 1891.
Phyllanthus euwensii Bold. Fl. Dutch W. Ind. **2**: 50–51, *pl. 4*. 1914.
Glochidion botryanthum (Muell. Arg.) Pax & Hoffm. Naturl. Pflanzenfam. ed. 2, **19c**: 58. 1931.

Glabrous shrub or small tree c. 1–4 m. high; branches slender, terete, furrowed, reddish-brown, c. 1.5–4 mm. thick; leader shoots up to 25 cm. long, lateral branchlets (of current year) c. 3–20 cm. long, with 5–15 leaves. Leaves: stipules triangular, mostly 0.8–1.1 mm. long and 0.5–0.6 mm. broad, acute, scarious, reddish- or blackish-brown, persistent (at least the basal portion), more or less entire. Petioles dark, grooved above, angled, 2.5–4 mm. long. Leaf-blades membranous or chartaceous, mostly ovate, c. (3–) 4.5–7.5 cm. long, (2–) 2.5–5 cm. broad, acute or obtuse (rarely emarginate) at the tip, obtuse or rounded at the base; above darkened in drying, the midrib and laterals very slightly raised; beneath more or less pruinose, the midrib salient, the laterals (c. 6–8 on a side) arching, slightly raised, branching to form a reticulum; margins unthickened, plane.

Monoecious; flowers mostly in bisexual cymules on leafless thyrses at distal nodes of ultimate axes; female flowers usually 1 or 2, males 3–6 per cymule, or the sexes more or less segregated onto different thyrses.

Male flower: pedicel capillary, c. 1 cm. long. Calyx-lobes 6, subequal, elliptic-oblong, c. 1–1.2 mm. long and 0.5–0.8 mm. broad, obtuse, purple-

stained except for the narrow scarious entire margins, midrib unbranched or nearly so. Disk-segments 6, massive, subcubical, foveolate, c. 0.3-0.4 mm. broad. Stamens 3; column c. 0.35–0.4 mm. high; anthers sessile, discrete, triangular, acute, c. 0.25–0.35 mm. long, 0.35–0.4 mm. broad; anther-sacs divergent, the slits not confluent, dehiscing horizontally; pollen grains mostly 22–26 μ in diameter, areoles oligobrochate, c. 5 μ across.

Female flower: pedicel capillary, (10–) 13–16 (–19) mm. long. Calyx-lobes 6, triangular-oblong, c. 1.2–1.3 mm. long and 0.7–0.8 mm. broad, acute or subacute, purple-stained as the male, the narrow scarious margin more or less entire, the midrib sparingly branched. Disk convex, extremely massive, circular or angled, nearly 2 mm. across, foveolate. Styles erect, connate or coherent into a column 0.3–0.45 mm. high, slightly dilated and merely truncate-emarginate at the apex.

Capsule oblate, trigonous, c. 3 mm. high and up to 6 mm. broad, somewhat rugulose, the veins obscure or conspicuous. Columella 1.7–2 mm. high. Seeds plano-convex, plump, umbonate (heliciform), 3.3–3.6 mm. long, 2.7–2.9 mm. broad, light brown, smooth (finely striolate).

Collected in flower and fruit May to January.

TYPE: Colombia, Carthagena, *Triana 3664* (P, LECTOTYPE; K, W, ISOTYPES).

DISTRIBUTION: coastal plain, northern South America (MAP XVIII).

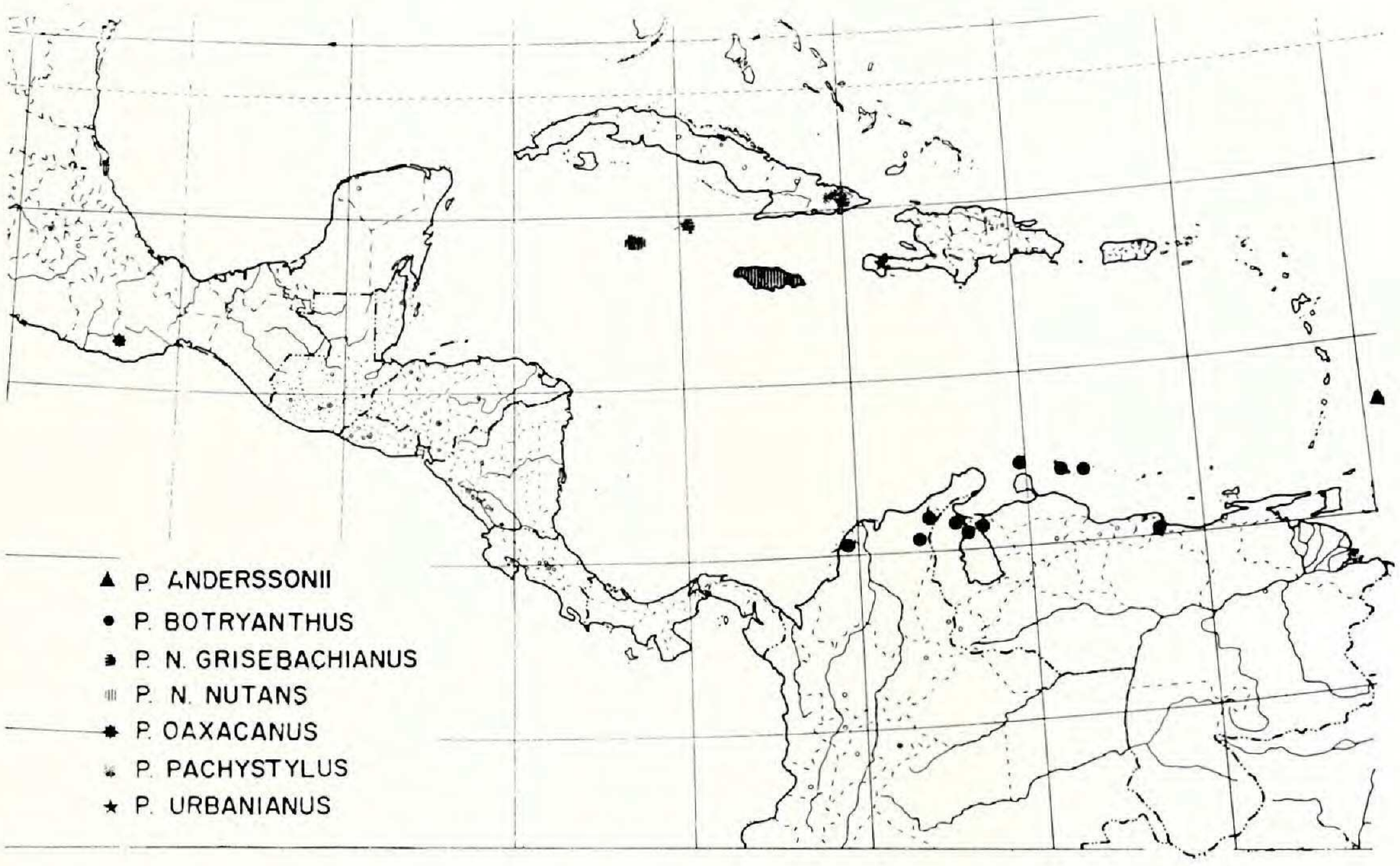
ARUBA: Kristalberg, 1885, *Suringar* (L). CURAÇAO: road near Antonyberg, *Boldingh 5141* (C); road near Wacao, *Boldingh 5252* (L); calcareous soil near San Pedro, *Boldingh 5279* (NY, ISOTYPE of *P. euwensii*); Tafelberg, *Curran & Hamman 164* (A); Hofje Abau, *Curran & Hamman 180* (A); rif-hospitaal, Hato, Savonet, *Suringar* (L). BONAIRE: klip Slachtbaai, *Suringar* (L). (Additional localities cited by Boldingh, loc. cit.)

The Curassavican plants represent merely a small outlying population of this species which is widespread and common in lowland areas along the northern coasts of Colombia and Venezuela. The specimens from the Dutch islands show no evident differences from the mainland plants, so that Boldingh's proposed *P. euwensii* cannot be maintained even at subspecific rank. Boldingh did not give any distinguishing characters for his intended new species, nor did he discuss its relationships; apparently he was unaware that the species also occurred on the mainland or that it had already received a name.

Because of its essentially entire styles associated in a column, *P. botryanthus* was placed by Mueller in his artificial sect. *Hemiphyllanthus*; it was therefore one of the species transferred to *Glochidion* by Pax and Hoffmann (loc. cit.), who arbitrarily assigned all species of *Phyllanthus* with entire styles to *Glochidion*. This betrayed mere bibliographic acquaintance with the plants, for *P. botryanthus* and *P. ovatus* (the other West Indian representative of Mueller's sect. *Hemiphyllanthus*) are neither closely related to one another nor to species of *Glochidion*.

The habit, floral structure, and pollen grains of *P. botryanthus* together

indicate an unquestionable relationship with the other species of sect. *Elutanthos*. Within the section, the closest West Indian relation appears to be *P. anderssonii*, which has very similar vegetative parts and male flowers but utterly different female flowers with bifid reflexed styles and a tenuous disk. In contrast, the female flowers of *P. botryanthus* are distinguished by the subentire erect styles and extraordinarily massive disk, which even in the bud stage is massive and swollen and which expands precociously to cause the calyx-lobes to become reflexed. However, the Mexican *P. oaxacanus* has a similar massive disk and, despite its very different styles, is probably the most closely related species.



MAP XVIII. Distribution of some Caribbean species of sect. *Elutanthos*.

44. **Phyllanthus anderssonii** Muell. Arg. in DC. Prodr. **15**(2): 395. 1866 (as *P. anderssoni*). (PLATE XXIV, *figs.* C–D).

Phyllanthus barbadensis Urb. Symb. Ant. **3**: 287. 1902.

A shrub c. 1 m. high [ex Eggers], with slender leader shoots up to c. 30 cm. long bearing distichous branchlets which terminate in naked thyrses (or leaders serving directly as thyrse-bearing axes); ultimate axes (branchlets) reddish brown, terete, sparsely to rather densely hirsutulous, mostly 4–10 cm. long, 0.6–1 mm. thick, with c. 6–15 nodes. Leaves: stipules triangular-lanceolate, 0.75–1 mm. long, 0.3–0.5 mm. broad, acute or acuminate, more or less hirsutulous, scarious, becoming reddish brown and at least the base persistent, entire or denticulate. Petioles dark and slender, flattened and hirsutulous adaxially, convex and glabrous abaxially, 1–1.8 mm. long. Leaf-blades membranous or chartaceous, elliptic to mostly ovate, c. 2.5–4.5 cm. long, 1.2–2.5 cm. broad, obtuse or subacute at the tip, cuneate at the base; above olivaceous or drying blackish,

hirsutulous proximally on the midrib but otherwise smooth and glabrous, nerves slightly raised; beneath glabrous, pale or pruinose, the midrib distinctly raised, the laterals (c. 7–10 on a side) ascending, slightly raised, connecting intramarginally, the tertiaries forming a rather inconspicuous reticulum; margins scarcely thickened, plane.

Monoecious; cymules mostly unisexual; male cymules several-flowered, borne at proximal axils of branchlet usually axillary to foliage leaves; female cymules with 1–4 flowers, borne on the thyrsiform terminal portions of branchlets (the leaves becoming more or less abruptly reduced to scales); one or two cymules at the transitional region often bisexual.

Male flower: pedicel capillary, up to c. 8 mm. long. Calyx-lobes 6, chartaceous, subequal, elliptic to oblong or obovate, c. 1–1.3 (–1.5) mm. long, 0.75–1 mm. broad, obtuse or subacute, entire or obscurely crenulate, the midrib unbranched. Disk-segments 6, very massive (about as large as the anthers), deeply furrowed and pitted, c. 0.3–0.4 mm. broad. Stamens 3; column c. 0.5–0.7 mm. high, c. 0.25 mm. thick; anthers sessile atop the column, discrete, the common connective convex, c. 0.2–0.3 mm. long and 0.35–0.4 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits not confluent; pollen grains c. 21–25 μ in diameter, areoles polybrochate, c. 5–7 μ across.

Female flower: pedicel slender, 7–13 mm. long. Calyx-lobes 6, subequal, ovate-oblong or obovate, 1–1.4 mm. long, 0.7–0.9 mm. broad, rounded or subtruncate at the tip, entire or obscurely crenulate, the midrib sparsely branching. Disk cupuliform, enclosing up to $\frac{1}{3}$ of the ovary, the tenuous rim crenulate, pitted. Styles connate or loosely coherent into a column c. 0.4–0.7 mm. high, the free ends sharply reflexed, bifid up to $\frac{2}{3}$ their length, the tips subulate, obtuse and entire or again emarginate or bifid.

Capsule oblate, trigonous, 6-sulcate, dark purplish brown, obscurely venose, c. 5.5–6 mm. broad, the valves c. 4.5 mm. long. Columella 1.8–2 mm. high. Seeds plano-convex, plump, umbonate, 2.7–3.3 mm. long, 1.7–2.3 mm. radially, 1.8–2.4 mm. tangentially, pale brown with very irregular longitudinal bands of slightly raised transversely elongated reddish-brown cells; hilum submedian.

Collected in flower Jan., Feb., June, Nov.; in fruit Feb., Nov.

TYPE: "Caracas," collector unspecified (Prodromus Herbarium, G, HOLOTYPE). The typification of this species is unfortunately fraught with difficulties which at this time cannot be wholly resolved. In Mueller's original description the origin of the type collection was indicated as follows: "Prope Caracas (hb. holm. sub n. 288! a cl. Dr. Andersson miss.)." Presumably the specimen was not collected by Andersson, since during his trip on the "Eugenie" he did not visit anywhere within the Caribbean area, his closest approach being the Pacific coast of Panama (cf. end-map in Skogman, Fregatten Eugenies Resa Omkring Jorden. 1854–55). If the plant was really collected near Caracas it seems unlikely that it could have escaped notice subsequently, although this cannot be entirely ruled out. It appears more likely that the specimen was actually obtained on Barbados

but was subsequently mislabelled. A search through the literature indicates that there is at least one possible source of the collection, for Robert Schomburgk spent several months on Barbados in 1846–47 and his citation (Hist. Barbados 593. 1848) of *P. nutans* can hardly refer to any species other than the present one. The figure "222" for the citation in Schomburgk's list does not agree with the "288" cited by Mueller, but the latter might be a field number. Of course, none of these circumstances constitutes proof that Andersson's specimen is a duplicate of a Schomburgk collection, so that it is impossible to decide conclusively whether the type collection of *P. anderssonii* is from Venezuela or from Barbados. Although it differs in a few minor particulars, the type specimen of *P. anderssonii* corresponds so well (e.g., in its hirtellous axes, massive male disk-segments, and sharply reflexed styles) with the specimens of *P. barbadensis* that it must be conspecific; and Mueller's name must thus take precedence over the much later one of Urban.

DISTRIBUTION: endemic to Barbados (MAP XVIII).

BARBADOS: Lion Hill Gully, St. James, *Dash 334* (NY); Forster Hall Wood, *Eggers 7130* (A, GOET, US; LECTOTYPE COLLECTION of *P. barbadensis*); Cole's Cave, St. Thomas, *Freeman & Bovell* (NY); Highland Gully, St. Thomas, *McIntosh* (K); Jack-in-the-box Gully and under Hackleton's Cliff, *Waby 15* (K); Bathsheba, *Warming 27* (C).

Beard (Nat. Veg. Leeward & Windward Isl. 166. 1949) has pointed out that practically all of the natural vegetation on Barbados has disappeared and that many plants endemic to Barbados have become extinct. However, since *P. anderssonii* has been collected at a number of different localities up to 1935, it seems possible that it may still survive, even though Beard failed to encounter it in his own reconnaissance of the island.

Urban compared *P. anderssonii* (as *P. barbadensis*) with *P. nutans*, to which indeed it shows some similarities; but its closest relationship is undoubtedly with *P. botryanthus*. In the face of their present distributions, the affinity between *P. anderssonii* and *P. botryanthus* has some anomalous aspects. It seems curious, for instance, that the female flowers (which are the best distinguishing character) of *P. botryanthus* are much more highly modified than those of *P. anderssonii*, for one might expect that it would be the latter, which presumably has been derived by colonization from South America, that would show the greater specialization. It also seems surprising that no related forms occur in a gap of about 500 miles between the state of Miranda, Venezuela (the easternmost known station for *P. botryanthus*) and Barbados. One possible explanation is that *P. anderssonii* may represent a relict of an extensive population which occupied the ancient land-mass of "Paria"; according to Schuchert (Hist. Geol. Ant.-Car. Reg. 19. 1935) this region extended from Maracaibo to Barbados at some time during the Cenozoic, but later foundered and is now represented only by some of the off-shore islands of northern South America.

45. **Phyllanthus nutans** Sw. Prodr. 27. 1788; Fl. Ind. Occ. 1103. 1800; Muell. Arg. in DC. Prodr. **15**(2): 375. 1866; Fawc. & Rend. Fl. Jam. **4**: 253–254. 1920.

Diasperus nutans (Sw.) O. Ktze. Rev. Gen. 2: 600. 1891.

A diffuse extremely variable shrub or slender tree 1–7 m. high, irregularly branching, the new axes borne distichously on older branches, often ending in nodding racemiform inflorescences, reddish brown, terete or angled, smooth or scabridulous or hirsutulous, 2–25 cm. long, 1–2.5 mm. broad, internodes 4–40 mm. long. Leaves: stipules scarious-chartaceous, deciduous or persistent, ovate to narrowly lanceolate, (2–) 3–5 (–9) mm. long, (1–) 1.5–4 (–6) mm. broad, obtuse to acute at the tip, truncate to cordate at the base, entire, yellowish, stramineous, or brownish. Petioles smooth or scabridulous to copiously hirsutulous, usually somewhat angled or margined, 1.5–4.5 mm. long. Leaf-blades chartaceous, quite variable in size and shape but most often ovate or elliptic, c. 3.5–8 (–11) cm. long, 2–5 (–8) cm. broad, obtuse or more rarely acute at the tip, cuneate to rounded at the base; above olivaceous, dull, the veins scarcely raised; beneath paler, sometimes glaucous or purplish-tinged, the midrib and lateral veins (5–8 on a side) raised, brownish or stramineous, the reticulum of veinlets usually conspicuous; margins unthickened, plane or revolute.

Monoecious; inflorescence variable; male cymules several-flowered, borne axillary or on pseudoterminal thyrses; female cymules 1–3-flowered, usually confined to the pseudoterminal thyrses (at least in ssp. *nutans*).

Male flower: pedicel capillary; 8–15 (–30) mm. long. Calyx-lobes 6, chartaceous, or somewhat fleshy, subequal, oblong to obovate, 2.3–3.2 mm. long, 1.3–2.2 mm. broad, rounded and obscurely crenulate or denticulate at the tip, often reddish at least below with thin creamy-yellow scarious margins but sometimes greenish throughout, the midrib with a few often conspicuous lateral branches. Disk-segments 6, thickened and fleshy, orbicular or reniform, obscurely to conspicuously foveolate-pitted, c. 0.35–0.7 mm. broad. Stamens 3; column c. 0.7–1.1 mm. high, tapering slightly to the apex; anthers sessile atop the column, discrete, usually deflexed but sometimes horizontal, broadly triangular to elliptic in outline, c. 0.4–0.6 mm. long and broad; anther-sacs slightly to markedly divergent, dehiscing horizontally or obliquely downwards, the slits confluent across the apex; pollen grains c. 21–26 μ in diameter, the areoles polybrochate, c. 6–8 μ across.

Female flower: pedicel terete, slender, smooth and glabrous or sometimes sparsely hirsutulous, reddish or olivaceous (sometimes pruinose), (6–) 10–27 mm. long. Calyx-lobes 6, erect at anthesis, biseriate, the outer elliptic-oblong and obtuse at the tip, the inner obovate and broader and more rounded at the tip; lobes 2–3.2 mm. long, 1–2.5 mm. broad, colored as the male, the scarcely raised midrib simple to conspicuously branched. Disk patelliform, fleshy, 6-angled or slightly lobed, foveolate. Styles erect, the undivided portions connate into a column 0.5–2.3 mm. high, the free

ends ordinarily sharply reflexed, bifid or parted nearly to the stylar column, the tips narrow or dilated, flattened, acute, 0.4–1.2 mm. long.

Capsule oblate-spheroidal, obscurely 6-ribbed, rounded in outline, c. 6 mm. high and 10 mm. broad, rugulose, the veins completely obscure. Columella c. 3–4 mm. high. Seeds trigonous (only slightly asymmetrical if at all), 4.2–7 mm. long, 2.8–4 mm. radially and tangentially, smooth, mottled light brown; hilum submedian.

Flowering probably throughout the year.

The populations of this extremely variable species of Cuba, the Cayman Islands, and Jamaica may be assigned to one or the other of the two following subspecies.

45a. **Phyllanthus nutans** ssp. **nutans** (PLATE XXIV, *figs.* E–F).

Phyllanthus nutans Sw. Prodr. 27. 1788.
Phyllanthus nutans β *purdiaeana* Baill. Adansonia **2**: 15–16. 1862.
Phyllanthus nutans var. *trojanus* Webster, Contr. Gray Herb. **176**: 47. 1955.

Stipules thin, usually precociously deciduous although conspicuous on young growth, ovate to lanceolate, (2–) 3–5 (–9) mm. long, (1–) 1.5–4 (–6) mm. broad, truncate or cordate at the base, glabrous, stramineous or greenish. Leaf-blades mostly ovate but often elliptic, glabrous beneath (except sometimes at the very base), usually obtuse or subacute at the tip and obtuse to rounded at the base; margins usually plane. Male cymules axillary or often at the proximal nodes of thyrses; female cymules 1–3-flowered, usually borne on more or less nodding pseudoterminal naked thyrses (i.e., ultimate axes with reduced leaves), sometimes the lowermost cymules in the axils of partially or wholly unreduced leaves. Calyx-lobes of male and female flowers subentire or obscurely denticulate, thickened at the base, the midrib simple or sparingly branched. Stylar column 0.5–2.3 mm. high; style-ends usually sharply reflexed, the lanceolate acute tips 0.4–1.2 mm. long.

TYPE: southern Jamaica, *Swartz*.

DISTRIBUTION: Jamaica and Cayman Islands (MAPS XVIII–XXI).

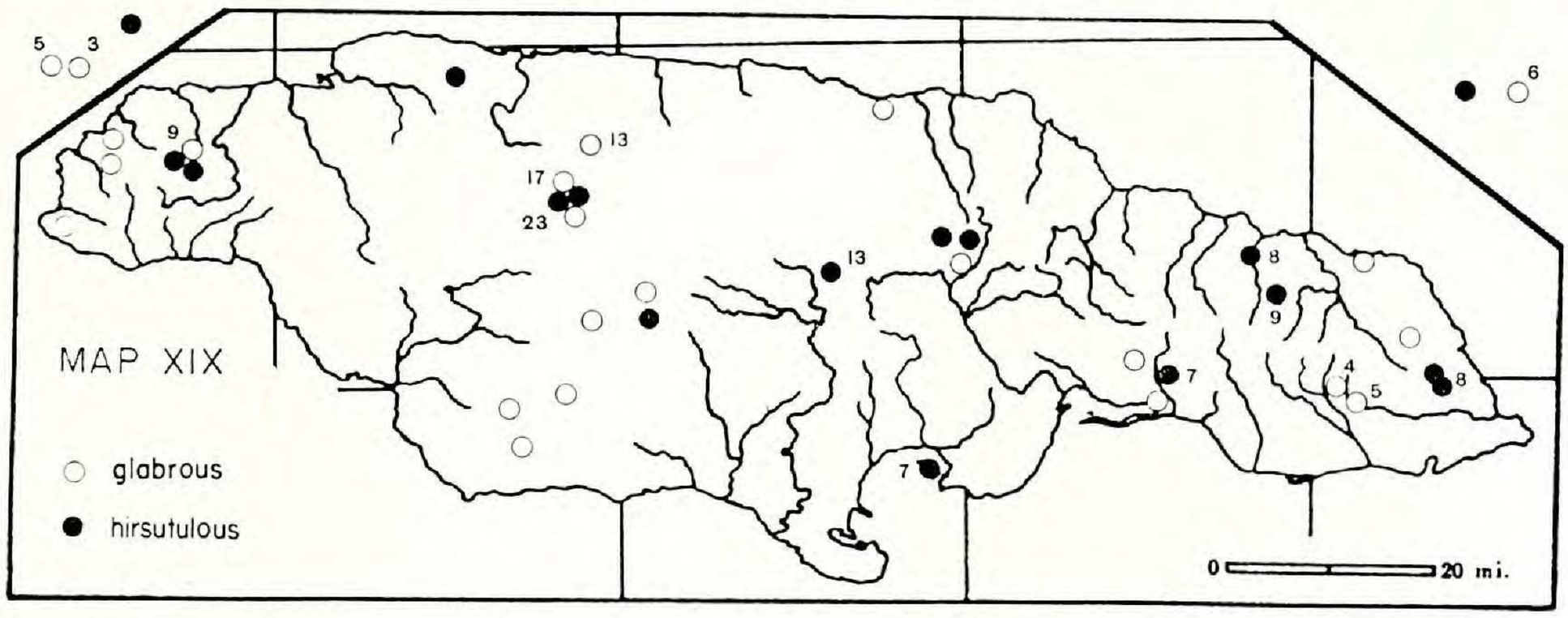
CAYMAN ISLANDS. GRAND CAYMAN: Grape Tree Point, dry rocky woodland, *Proctor 11977* (GH); between Old Isaacs and Wintersland, *Proctor 15245* (GH).

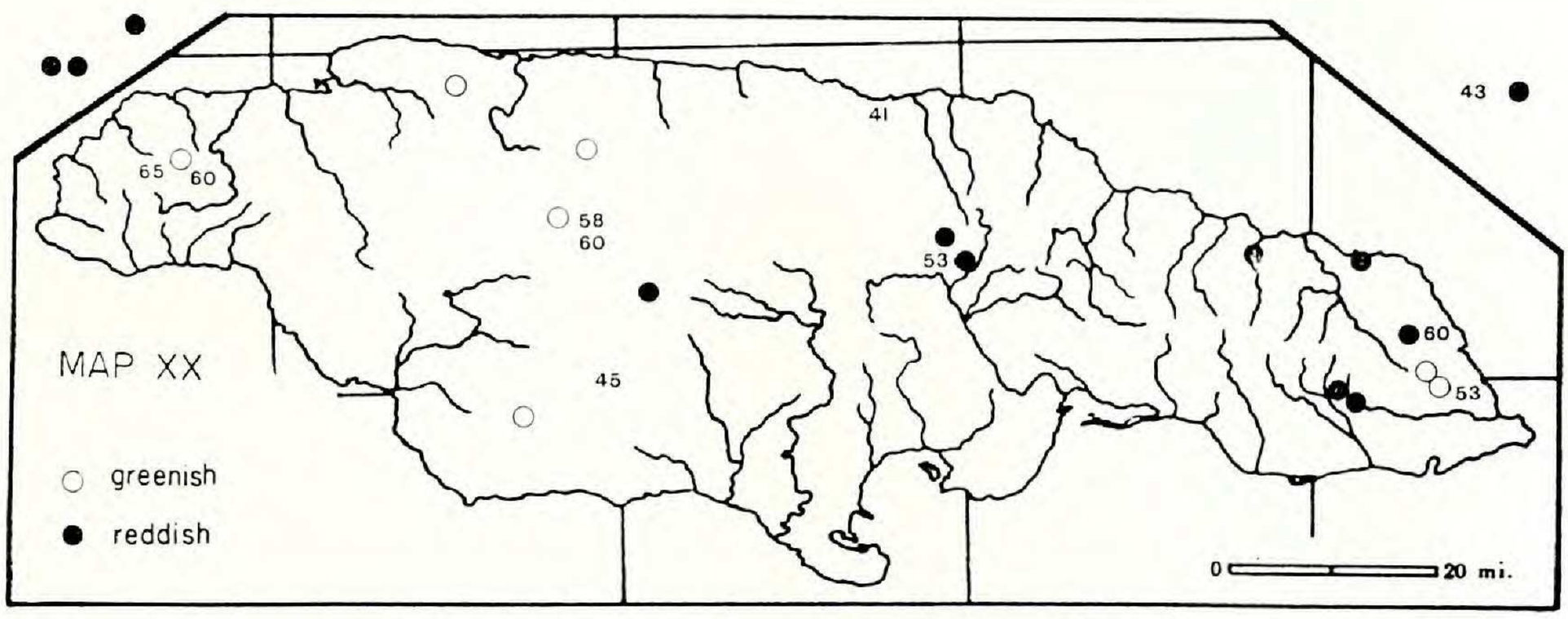
JAMAICA. Without locality: *Alexander* (A, GOET), *Hooker* (W), *Jacquin* (W), *Swartz* (S, HOLOTYPE; A, C, G, P, S, ISOTYPES), *Wilson 232* (NY), *Wullschlaegel s.n.* (GH), *900*, *1053*, *1114* (GOET), *1318* (W). HANOVER: Fish River Mountains, *Britton & Hollick 2167*, *2170* (F, NY), *Harris 10260* (F, NY, US); Dolphin Head, *Britton 2314* (F, NY), *Harris 10309* (F, US), *Webster & Wilson 5075* (A, JAM). WESTMORELAND: Negril, rocky wooded hills, *Britton & Hollick 2082* (NY). ST. JAMES: Chatham, alt. 300 m., *Guilbride & Barkley 22J174* (MICH). ST. ELIZABETH: Potsdam woodland, *Harris 9778* (F, US); New Buildings, south of Gutters, *Howard & Proctor 14992* (A); Santa Cruz Mountains, near Hampton School, alt. 2400 ft., *Webster & Proctor 5293* (A, JAM). TRELAWNY: Ramgoat Cave, *Howard 14129* (A); Tyre, alt.

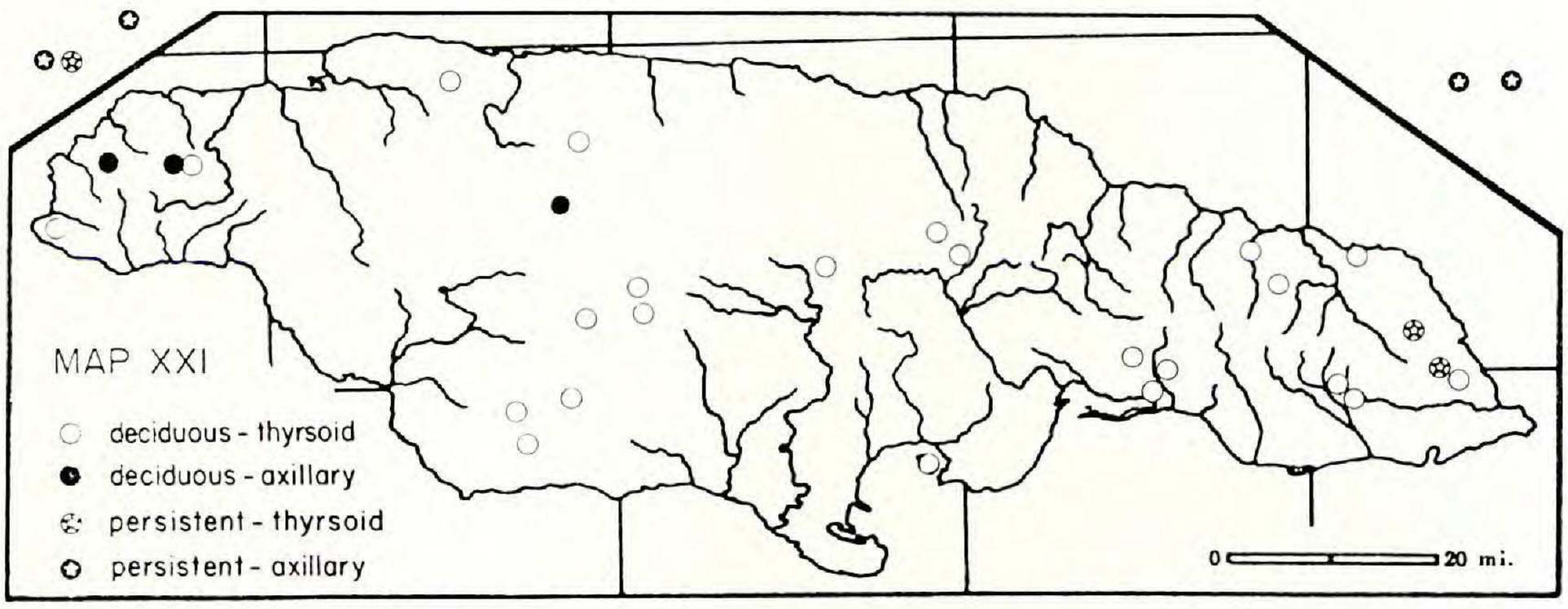
1750 ft., *Proctor 9936* (GH); road to Troy, *Harris 8687* (F, NY, US); Troy and vicinity, *Britton 929* (NY), *Perkins 1331* (GH, HOLOTYPE of var. *trojanus*). MANCHESTER: Brown's Town to Porus, hillside, *Britton 3272* (F, NY); vicinity of Mandeville, *S. Brown 248* (A, NY); 1.5 miles north of Shooters Hill, *Howard 14107* (A). ST. ANN: interior of St. Anns, *Purdie* (P, type collection of var. *purdiaena*); Guys Hill, Moneague, *Alexander* (G); Union Hill, near Moneague, *Britton & Hollick 2747* (F); Discovery Bay, *Hunnewell 18844* (GH). CLARENDON: Croft's Mountain, alt. 2500 ft., *Harris 11212* (F, NY). ST. CATHERINE: Old Harbour Bay, Little Goat Island, rocky woods, *Britton & Hollick 1855* (F, NY); Great Goat Island, southeastern side, *Harris 9301* (A, C, JAM, NY), *9337* (A, C, NY); Devil's Race Course, *Proctor 7213* (MICH). ST. ANDREW: valley of Yallahs River, *Alexander* (NY); Rock Fort, *Campbell 6412* (NY); near Hope, *Harris 8601* (JAM, NY), *8950* (JAM, NY, US); Hope River gorge, August Town, *Powell 297* (A). PORTLAND: Swift River gorge at Eden, *Proctor 11868* (GH); Uncommon Hill, *Proctor 8555* (GH); Port Antonio, Cave Hill near railway station, *Wight 199* (F, NY); John Crow Mountains, above Ecclesdown, rain-forest, *Howard, Proctor & Stearn 14769* (A). ST. THOMAS: Mansfield, *Britton 3557* (NY); Golden Valley, *Harris 5423* (F, NY); Plantain Garden River gorge, northwest of Whitehall, *Proctor 7419* (GH); Whitehall to Big Hill, *Proctor 7671* (JAM); Big Level, southeast end of John Crow Mountains, *Proctor 11820* (GH), *Webster & Proctor 5516* (A, BM, JAM, MICH, US).

Not only is *P. nutans* one of the most variable of the West Indian species, but its Jamaican representative (ssp. *nutans*) is certainly one of the most widespread woody plants on that island; it occurs from sea-level (at Rock Fort) to 2,500 ft. in the hills of the interior, and from such arid localities as Great Goat Island to dripping rain forest in the John Crow Mountains where the precipitation certainly exceeds 200 inches per year. The only sizeable area on the island where it appears to be absent is the upper slopes of the Blue Mountains (above 3,000 ft.); although it has most often been collected on limestone, it has also been found growing on serpentine (e.g., *Proctor 7419*).

In view of its ubiquitous distribution on Jamaica, it is not surprising that ssp. *nutans* should exhibit so much variability; but any attempt to categorize these variations can only encounter great difficulty. Even the distinction between the two subspecies is not very well-marked and may prove to be untenable when more collections are available from the Cayman Islands and Cuba. Since it has not proved very useful to express the intraspecific variation in terms of conventional taxa, a series of maps plotted for individual characters has been prepared. Many characters, of course, show a purely random distribution, as Map XIX shows for the presence or absence of pubescence. It is curious, however, that in the related species of this section, *P. barbadensis* and *P. botryanthus*, there is no variation in this respect, all individuals being hirsutulous and glabrous respectively. The distribution of reddish color in the calyx, plotted on Map XX, is a somewhat more doubtful case, for it might appear that there is a bicentric distribution of green calyces; however, the number of samples is small (due to the difficulty in ascertaining the color if there







MAPS XIX–XXI. Distribution of certain morphological characters in populations of *Phyllanthus nutans* Sw. The symbols separated by heavy lines in the upper left-hand and right-hand corners refer to the disjunct populations in the Cayman Islands and eastern Cuba, respectively. The numbers associated with the dots in Map XIX indicate the mean stylar length (in tenths of a millimeter) of the individual samples, while the numbers in Map XX refer to the mean seed length in tenths of a millimeter. All herbarium specimens from definite localities are plotted in Map XIX, but some of these do not appear in Maps XX and XXI because of incomplete data.

are no label data) and it seems likely that further collections may break down the apparent distinction.

There are, however, a number of characters which show undoubted geographically correlated variation and it might be thought that these could serve as the basis for the recognition of subspecies or varieties. For instance, it is quite evident that in seed size, length of stylar column, and inflorescence-type the plants from the western part of the island show differences from the eastern populations. But a closer inspection will show that although there is a *general* east-west separation (and this holds, on a larger scale, between Jamaica and Cuba), the characters vary independently of one another to such an extent that no satisfactory minor taxa can be defined within the Jamaican plants as a whole. Thus var. *trojanus*, which was previously defined on the basis of plants with a long stylar column, must be relegated to synonymy, for the plants from Dolphin Head which otherwise agree with the plants from Troy in their inflorescence and leaves have much shorter stylar columns. The var. *purdiaeanus* recognized by Baillon and Mueller is an even less significant variation (of conspicuously bracteate inflorescences) which has a purely random distribution.

The two most striking character differences within *P. nutans* certainly deal with the stipule and inflorescence types, and it is indeed upon this fact that the two subspecies are recognized. It must be admitted, however, that even here the correlation is far from perfect. The Cuban ssp. *grisebachianus* clearly differs from most forms of ssp. *nutans* in its solitary axillary flowers and persistent stipules; but some plants in western Jamaica have essentially axillary flowers, while in the Cayman Islands and in the John Crow Mountains at the eastern end of Jamaica occur some anomalous forms with persistent stipules but which in other respects are more or less typical for ssp. *nutans*. It is clear, in the case of the John Crow plants, that the persistent stipules have been derived independently of those in ssp. *grisebachianus*; and a collection from the central part of the John Crow range (*Howard & Proctor 14769*) is furthermore so divergent that it was at first thought to represent a distinct species. In this collection the leaves are conspicuously corrugated, quite unlike any other specimens of *P. nutans*, even though the difference becomes obscured in drying. However, the inflorescence is typical for ssp. *nutans*, and the persistent stipules are shared by a collection from the Big Level area of the John Crow Range (*Webster & Proctor 5516*) which seems otherwise to represent ssp. *nutans*. Thus, despite the importance of the morphological divergence in the John Crow Mountains population, it does not seem practicable to designate it as a species or even subspecies.

The plants from the Cayman Islands, although not showing any divergence as extreme as the bullate-leaved form from the John Crows, are of great interest in that they bridge rather nicely the gap between the two subspecies. The two collections from Grand Cayman seem assignable to ssp. *nutans* by virtue of their ovate leaves, but they are to some extent transitional, because *Proctor 15245* has the axillary flowers of ssp. *grisebachianus* combined with the deciduous stipules of ssp. *nutans*, while

Proctor 11977 has the thyrsoid flowers of ssp. *nutans* combined with apparently persistent stipules as in ssp. *grisebachianus*. The collection from Little Cayman (*Kings LC42*), on the other hand, is clearly referable to ssp. *grisebachianus*, since it has elliptic, revolute leaves, persistent brownish stipules, and flowers axillary (or mostly so). While it is perhaps arbitrary to assign the Grand Cayman plants to ssp. *nutans*, there is in any event no doubt that the Cayman Islands population forms a connecting link between the two subspecies. Possibly the key to understanding the present distribution of *P. nutans* lies in the geological history of the Cayman Islands.

45b. **Phyllanthus nutans** ssp. **grisebachianus** (Muell. Arg.) stat. nov. (PLATE XXIV, *figs.* G–H).

Phyllanthus grisebachianus Muell. Arg. Linnaea **32**: 26. 1863; DC. Prodr. **15**(2): 380. 1866.
Diasperus grisebachianus (Muell. Arg.) O. Ktze. Rev. Gen. Pl. **2**: 599. 1891.

Stipules scarious, chartaceous, persistent (at least the basal portion), lanceolate, 2–3.5 mm. long, 0.7–1.5 mm. broad, truncate at the base, glabrous or hirsutulous, dark brown. Leaf-blades elliptic, glabrous or hirsutulous beneath, acute at tip and base, margins narrowly revolute. Flowers entirely axillary, solitary or the male and female paired at each axil. Calyx-lobes of male and female flowers denticulate, thin, the midrib conspicuously branched. Stylar column c. 0.5–0.7 mm. high; style-ends reflexed, dilated, bifid or notched, the tips recurved. Seeds c. 4.5 mm. long.

TYPE: eastern Cuba, *Wright 582*.

DISTRIBUTION: eastern Cuba (Sagua-Baracoa range) and Cayman Islands (MAPS XVIII–XXI).

CAYMAN ISLANDS: Little Cayman, South Town, *Kings LC42* (BR, NY). CUBA. ORIENTE: "Cuba Orientali," *Wright 582* (G, HOLOTYPE; A, BR, G, GH, GOET, ISOTYPES); Monte Verde, 10 May 1859, *Wright 1436* ex. p. (BR, G, GH, S; mixed in some collections with *Margaritaria scandens*).

As here circumscribed, ssp. *grisebachianus* is readily distinguishable from ssp. *nutans* except in the Cayman Islands. The association of the Kings collection from Little Cayman with ssp. *grisebachianus* rather than with the Grand Cayman plants (which are assigned to ssp. *nutans*) is based on its pointed revolute leaves hirsutulous beneath (on the midrib) and its dark persistent stipules. However, it must be granted that the Little Cayman specimen shows several discrepancies as compared with the Cuban plants, for it has female pedicels 15–30 mm. long and female flowers which are neither all solitary nor all axillary to unreduced leaves, whereas the Cuban collections show pedicels 6–14 mm. long and have completely solitary, axillary flowers. The population on Little Cayman may, therefore, be classified as transitional between the two subspecies but with the stronger leaning to ssp. *grisebachianus*, whereas the Grand

Cayman plants fall closer to ssp. *nutans*. Additional collections, particularly from Cayman Brac and from Cuba, might provide a decisive test of the practicability of the present classification. It may prove to be unfeasible to maintain two subspecies if additional break-down in the characters is shown to exist; but, for the present, the Cuban and Jamaican populations appear to be sufficiently distinct from one another to warrant separation.

46. **Phyllanthus pachystylus** Urb. Symb. Ant. 3: 286. 1902. (PLATE I, *fig. 2*; PLATE XXIV, *figs.* I–L).

A slender sparsely branching shrub (usually with a single main stem) becoming 1–1.5 m. high; main stem 3–5 mm. thick, terete, bark burnished and reddish brown becoming greyish and fissured; branches mostly steeply ascending, reddish brown angled, furrowed, glabrous or rarely hirsutulous, becoming mostly 8–25 cm. long, c. 1.2–2.5 mm. thick, with c. 5–15 nodes. Leaves: stipules lanceolate to linear-lanceolate, (1.2–) 1.5–2 (–3) mm. long, 0.4–1 mm. broad, acute, glabrous, becoming darkened and indurate, persistent, entire. Petioles stout, glabrous or rarely hirsutulous, 2.5–5 mm. long. Leaf-blades becoming rigidly coriaceous, mostly elliptic-oblong (varying to narrowly elliptic, ovate, or lanceolate), mostly 3.5–7 (–9) cm. long, (1–) 1.5–3.5 (–4.5) cm. broad, obtuse, rounded, or retuse at the tip, acute to obtuse at the base; above dark purplish (drying blackish) when young, becoming more or less olivaceous-plumbeous, essentially smooth (often somewhat wrinkled), the midrib and lateral veins noticeably sunken; beneath much paler, alveolar-pruinose, the midrib prominently raised, the spreading to ascending laterals (5–7 on a side) somewhat raised, the reticulum of veinlets often visible; margins thickened, conspicuously revolute.

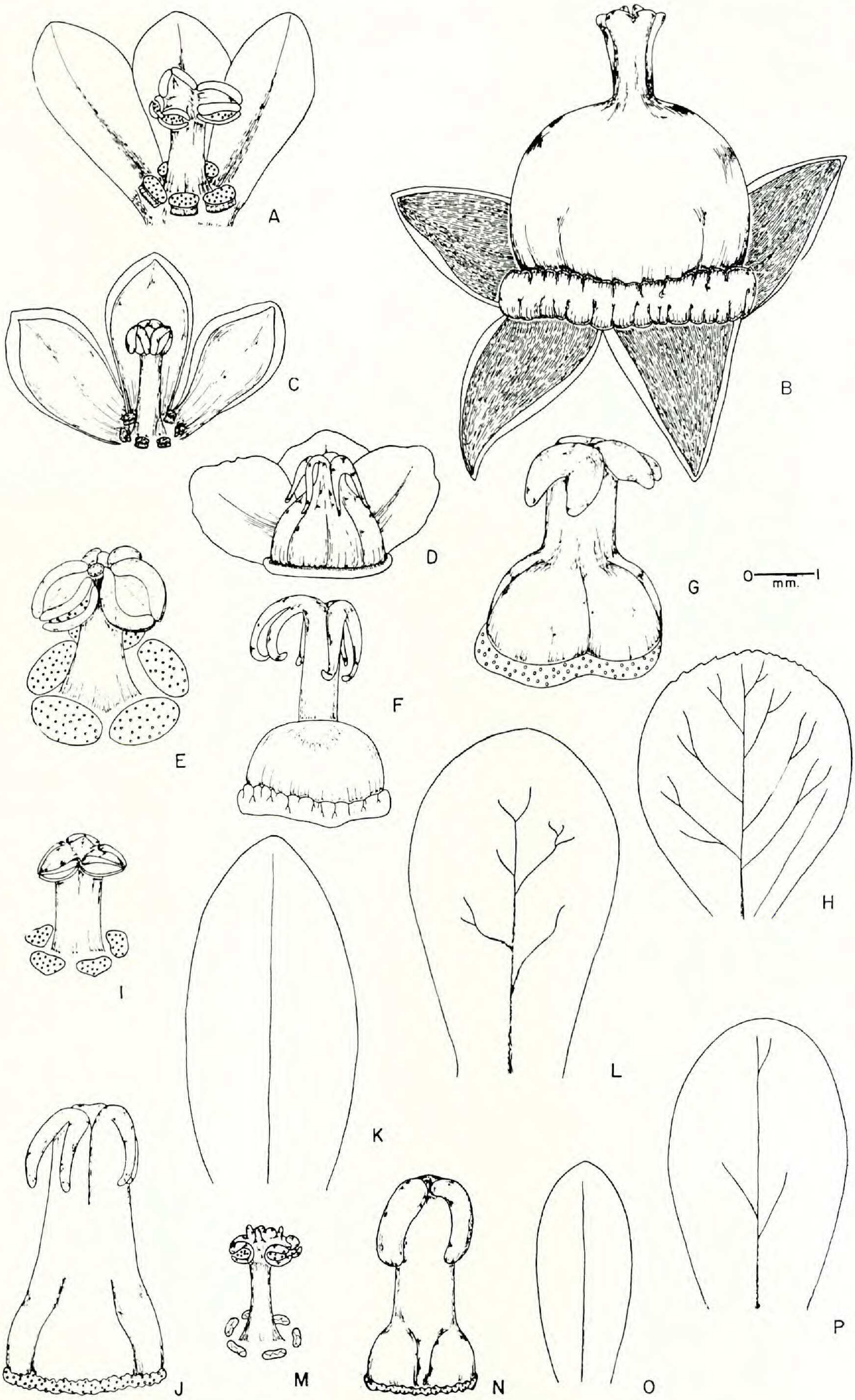
Monoecious; cymules mostly bisexual, each with 1–3 female and 2–10 male flowers, in the axils of bracts on naked pseudo-terminal thyrses (the thyrses produced from one or several axils immediately below the tip of the branchlet); cymules sometimes unisexual.

Male flower: pedicel capillary, smooth or rarely hirsutulous, 7–12 mm. long. Calyx-lobes 6, rather fleshy, biseriate (but sometimes obscurely so),

---

PLATE XXIV. FLOWERS OF SECT. *Elutanthos*.

FIGS. A–B. Male and female flowers of *Phyllanthus botryanthus* Muell. Arg. (*Haught 6556* [GH]). FIGS. C–D. Male and female flowers of *Phyllanthus anderssonii* Muell. Arg. (*Warming 27* [C]). FIGS. E–F. Androecium and gynoecium of *Phyllanthus nutans* Sw. ssp. *nutans* (*Proctor 15245* [GH], *Webster & Wilson 5075* [A]). FIGS. G–H. Gynoecium and female calyx-lobe of *Phyllanthus nutans* ssp. *grisebachianus* (Muell. Arg.) Webster (*Wright 1436* [S]). FIGS. I–L. Androecium, gynoecium, inner and outer female calyx lobes of *Phyllanthus pachystylus* Urb. (androecium, *Howard 6199* [GH]; others, *Ekman 15037* [S]). FIGS. M–P. Androecium, gynoecium, and inner female calyx-lobes of *Phyllanthus urbanianus* Mansf. (*Ekman H10435* [S]).



WEBSTER, WEST INDIAN PHYLLANTHUS

(2–) 2.3–3 mm. long, outer lobes usually oblong and obtuse, c. 1.3–1.6 mm. broad, with midrib simple or nearly so, inner lobes usually obovate, c. 1.5–2 mm. broad, with midrib usually sparsely branched (occasionally simple); lobes entire or sparsely denticulate. Disk-segments 6, usually rather massive, reniform to elliptic, foveolate, c. 0.3–0.6 mm. across. Stamens 3; column rather stout, (0.6–) 0.75–0.9 (–1) mm. high, mostly 0.4–0.6 mm. thick; anthers sessile atop the column, basally connate, the common connective plane or umbonate, triangular, c. 0.3–0.55 mm. long and 0.4–0.6 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits not confluent; pollen grains c. 21–24 μ in diameter, areoles polybrochate, c. 4–6 μ across.

Female flower: pedicel slender, terete, more or less reddish, glabrous or rarely hirsutulous, 2.5–6 (–8) mm. long, 0.3–0.5 mm. thick. Calyx-lobes 6, distinctly biseriate, (2–) 2.5–3.5 (–4) mm. long, entire or obscurely denticulate; outer lobes narrowly oblong with midrib almost or quite unbranched (rarely copiously pinnately branched), c. 1–1.5 (–1.9) mm. broad; inner lobes obovate or spathulate with midrib always pinnately branched, c. 1.4–2.2 mm. broad; lobes entire or obscurely denticulate. Disk shallowly cupuliform, angled, finely crenulate. Styles connate or coherent into a massive column (0.5–) 0.7–1 (–1.5) mm. high which is not sharply demarcated from the ovary; free ends of styles recurved, 0.4–0.6 (–0.9) mm. long, more or less dilated, parted ½ to ¾ their length, the tips broadly triangular to lanceolate, obtuse to acute.

Capsule rounded in outline, c. 5 mm. high and 8 mm. broad, rarely remaining entire, the valves rugulose. Columella rather massive, (3–) 4 (–4.5) mm. high. Seeds trigonous, nearly symmetric, (4–) 4.5–5.4 mm. long, 2.7–3.1 mm. radially, 2.9–3.5 mm. tangentially, light brown, smooth (very finely striolate); hilum submedian; micropylar end sometimes developing a conspicuous whitish caruncle.

Collected in flower and fruit April through September.

TYPE: Cuba, Oriente, *Wright 1947*.

DISTRIBUTION: endemic to the Sagua-Baracoa massif, eastern Cuba (MAP XVIII).

CUBA. ORIENTE: Sierra de Nipe, near Río Piloto, *Ekman 2274, 6028, 15037* (S); Charrascal de la Cueva, Mayarí, *León et al. 19888* (MICH); wooded hillside, San José, *Howard 6199* (GH, NY); near Woodfred, deciduous woods and thickets, *Shafer 3617* (NY); edge of savannas near Sagua de Tánamo, 3 April 1861, *Wright 1947* (GH, LECTOTYPE; G, GOET, ISOTYPES); pinares near Moa, *Acuña 12503* (US), *Bucher 102, 107* (NY), *Clemente 3555* (MT), *Marie-Victorin et al. 21565* (A, MT), *21705* (MT); Franklyn Mine, *Clemente & Alain 3890* (MICH); Playa La Vaca, *Clemente 4918* (MICH); Cerro de Miraflores, *Marie-Victorin et al. 21557* (A, MT); dense pine woods 15 kms. southwest of Moa mill, *Howard 5955* (GH); pinelands on serpentine between Río Moa and Río Yagrumaje, *Webster 3757, 3771* (MICH); Cayo Chiquita, 8 km. south of Moa, *Webster 3848* (GH, MICH); pine scrub 10 km. south of Moa, *Webster 3895* (GH, MICH); scrublands 16 and 18 km. south of Moa, *Webster 3906, 3907* (GH, MICH).

This species has a very characteristic appearance in the field due to its shiny, coriaceous, purplish leaves and nodding inflorescences which may even be twining in dense undergrowth. Unlike the other West Indian species of sect. *Elutanthos*, which are predominantly calciphiles, *P. pachystylus* appears to be confined to serpentine; and like many species in other genera growing on the limonite soils of the Moa region, it shows a greater degree of apparent morphological adaptation to dry conditions than do its related congeners. Ekman noted on his labels that in the Sierra de Nipe the species is rare and becoming extinct; but in the Moa area it is certainly still thriving and in fact is one of the commonest undershrubs in the open pinelands there.

The closest relationship to *P. pachystylus* appears to be shown by *P. nutans* ssp. *grisebachianus*, which occupies a clearly allopatric range in the Monte Verde area, although the gap in range may be no more than about 20 or 25 miles. The thinner stipules and leaf-blades, solitary axillary flowers, longer female pedicels, and less massive styles of that plant present so many distinctions that there can be no doubt as to the specific distinctness of *P. pachystylus*.

47. **Phyllanthus urbanianus** Mansf. Repert. Sp. Nov. 32: 86. 1933. (PLATE XXIV, *figs.* M–P).

A small shrub (probably with the aspect of *P. pachystylus*); main stem subsimple, c. 2.5 mm. thick, terete, bark dark reddish brown, reddish hirsutulous; ultimate branches reddish brown, terete, somewhat furrowed, reddish hirsutulous, c. 20–35 cm. long, 0.9–1 mm. thick, with c. 20–45 nodes. Leaves: stipules narrowly lanceolate, 1.2–1.8 mm. long, 0.25–0.5 mm. broad, acute, thin and scarious, olivaceous becoming dark brown and persistent. Petioles rather slender, reddish- or hyaline-hirsutulous, c. 3–4 mm. long. Leaf-blades chartaceous, elliptic, c. 4–6.5 cm. long and 1.2–2.7 cm. broad on main stem, decreasing to 1.5–3 cm. long and 0.4–1.2 cm. broad at tips of branches, acute at the tip, acute to obtuse at the base; above dark olivaceous, reddish hirsutulous along the scarcely raised midrib and laterals; beneath pale, copiously hirsutulous throughout, the midrib and laterals (4 or 5 on a side) raised, light brownish; margins unthickened, narrowly revolute.

Monoecious; cymules mostly bisexual, each with a single central female flower and several lateral males, in the axils of semi-reduced (still leaf-like) bracts on distal branches (which are homologous with the "naked" thyrses of *P. nutans*); individual cymules occasionally replaced by depauperate inflorescence axes.

Male flower: pedical capillary, smooth to copiously hirsutulous, c. 8–10 mm. long. Calyx-lobes 6, c. 2.2–2.5 mm. long, more or less biseriate: outer lobes narrowly oblong, c. 0.75 mm. broad, inner lobes elliptic-oblong, slightly over 1 mm. broad; lobes all rounded at the tip, reddish with rather ill-defined yellowish margins, the midrib simple or sparingly branched. Disk-segments 6, flattened, roundish, foveolate, c. 0.2–0.3 mm. across.

Stamens 3; column c. 0.8 mm. high, slightly constricted above; anthers sessile, c. 0.25 mm. long and 0.4 mm. broad, alternating with three erect apiculae c. 0.2 mm. long; anther-sacs rather broadly divaricate, dehiscing horizontally; pollen grains 18–21 μ in diameter, areoles transitional between oligobrochate and polybrochate, c. 4–6 μ across.

Female flower: pedicel slender, terete or nearly so, sparsely to copiously hirsutulous, 12–15 mm. long. Calyx-lobes 6, biseriate: at anthesis, outer lobes linear-oblong, obtuse, with simple midrib, 2–2.3 mm. long and 0.8–0:9 mm. broad, inner lobes obovate, rounded at the tip, with sparingly branched midrib, 2.7–3 mm. long and 1.3–1.5 mm. broad; lobes chartaceous, reddish, essentially entire, becoming reflexed in fruit. Disk shallowly cupuliform, 6-angled, rather fleshy, crenulate. Styles connate into a massive column c. 1 mm. high and 0.5 mm. broad; free ends of styles recurved, dilated, oblong, obtuse or emarginate, c. 0.4–0.6 mm. long.

Capsule c. 4 mm. high and 7 mm. broad, somewhat rugulose. Columella c. 2.5 mm. high. Seeds trigonous, slightly asymmetric (somewhat umbonate at one corner), c. 4.2 mm. long, 2.7 mm. radially, 2.9–3 mm. tangentially, smooth, mottled light brown; hilum submedian.

TYPE: Haiti, Dept. Sud, Massif de la Hotte, western group, Les Roseaux, Hab. Gros-Roche, rocky forest, hard limestone, alt. 400 m., rare, 27 June 1928, *Ekman H-10435* (S, HOLOTYPE; A, US, ISOTYPES).

DISTRIBUTION: known only from the type collection (MAP XVIII).

This rare endemic species is of particular phytogeographic interest, because it is the only representative of the section on Hispaniola. It resembles both *P. pachystylus* and *P. nutans* (especially ssp. *grisebachianus*), but differs in its more hirsutulous parts and very distinctive staminal column and styles, so that there would appear to be no reason to question its specific distinctness. The Cuban and Jamaican affinities of *P. urbanianus* provide another good demonstration (in addition to species relationships in sects. *Cyclanthera* and *Hemiphyllanthus*) of the profound floristic division between the Sellean peninsula of Haiti and the remainder of Hispaniola.

Subgenus VIII. **Xylophylla** (L.) Pers. Syn. Pl. 591. 1807; emend.

Xylophylla L. Mant. 2: 147–148. 1771.

Trees or shrubs with phyllanthoid branching, the branchlets pinnatiform or bipinnatiform; monoecious or very rarely dioecious. Male flower; calyx-lobes 4–6; disk of as many segments, these free or united; stamens 2–15, free or more commonly united; anthers dehiscing vertically to horizontally; pollen grains globose, areolate. Female flower: calyx-lobes 5 or 6 (rarely 4); disk cupuliform or patelliform; ovary of 3 carpels; styles bifid or multifid, sometimes dilated at the tips. Fruit capsular; seeds 2 in each locule.

Included in this large, entirely American subgenus of about a dozen sections and 60 species are the majority of the neotropical woody species

of *Phyllanthus*. The West Indies are definitely the center of distribution and apparently also of the evolution of the group, but a few additional sections (e.g., *Oxalistylis* and *Ciccastrum*) are confined to South America. In Mueller's treatment in the "Prodromus" the sections and species here brought together were much scattered, the following of his sections belonging (at least in part) to subg. *Xylophylla*: 12, 16–19, 34 (in small part), 35–36, and 44. Persoon's original conception of subg. *Xylophylla* as including only the phylloclade-bearing species was of course much narrower than that here adopted, and in fact corresponds to sect. *Xylophylla* alone.

Because of the dominant position of representatives of subg. *Xylophylla* in the West Indies, its relationships are of particular interest. However, although certain lines of affinity are very apparent within the group, there are several unresolved problems which make impossible an accurate tracing of phylogeny. It is certain that there is a close relationship between subg. *Xylophylla* and subg. *Botryanthus*, and the approach is nearest between sects. *Asterandra* and *Elutanthos*, respectively. Some of the Central American species of sect. *Elutanthos* (e.g., *P. grandifolius*) resemble sect. *Asterandra* so clearly that there can be little doubt of a significant kinship. However, there are some obstacles, to be discussed more fully farther on, which make it at least uncertain that subg. *Xylophylla* can be directly derived from subg. *Botryanthus* via sect. *Asterandra*. The small number of stamens in the flowers of *Botryanthus* and the large capsule of such species as *P. grandifolius* are features which appear to be derivative; so that it is possible to read the evolutionary series the other way around and to postulate that subg. *Botryanthus* has been derived from sect. *Asterandra* by reduction in the androecium accompanied by loss of phyllanthoid branching and increase in fruit size.

Within subg. *Xylophylla* two main phyla can be discerned: a series beginning with sect. *Williamia* and running through sects. *Thamnocharis* and *Orbicularia*; and a series proceeding from sect. *Asterandra* to sects. *Epistylium*, *Hemiphyllanthus*, and *Xylophylla*. Standing alone is sect. *Omphacodes*, which is aberrant in many respects and which in fact resembles sect. *Ciccopsis* of subg. *Cicca* more than it does any single section of subg. *Xylophylla*. It is classified here because of its areolate pollen grains, but without strong conviction, and its relationships need to be further investigated.

The initial dichotomy between sect. *Williamia* and sect. *Asterandra* has some puzzling aspects which cannot yet be resolved. That the higher stamen number in *Williamia* may be a primitive character is attested by the clearly documented reduction-series to a lower number in the derived sections; furthermore, the seeds of *Williamia* are less highly modified than those of *Asterandra*. However, the South American sect. *Oxalistylis*, which is closely related to *Asterandra*, has more unspecialized seeds, and perhaps can be thought of as a group more or less coördinate with *Williamia*, if indeed the two are not descended from some immediate common ancestor.

The anatomical evidence from leaves, as shown earlier in this study

(Jour. Arnold Arb. 37: 220. 1956), demonstrates for many taxa of this subgenus an interesting correlation between floral modification and increasing sclerification of foliar tissue. The rationale for this would appear to be that the evolutionary history of many of the groups of subg. *Xylophylla* has been one of increasing adaptation to xeric conditions. However, the adaptive radiation has been rather complex, so that no over-all generalizations on the ecology of the species can be made. In both the *Williamia* and *Asterandra* lines, however, the end-products of evolution (viz., sects. *Orbicularia* and *Xylophylla*) comprise species so altered in appearance that their ancestry could scarcely be guessed if it were not possible to trace it back through intervening species.

KEY TO THE SECTIONS

1. Branchlets pinnatiform.
   2. Styles each terminating in a dilated more or less crenate to lacerate stigma.
      3. Disk-segments of male flower free or at least not completely united; seeds thin-walled, neither fissured nor mottled; petioles without undulate marginal ridges.
         4. Leaves obtuse or emarginate at the tip; styles not calyptriform or if so then branchlet leaves opposite; stamens 3–15. . . 16. **Williamia**
         4. Leaves acuminate; styles calyptriform or united into a massive column; stamens 2 or 3 (rarely 4); at least some inflorescences cauliflorous (except in *P. axillaris*). . . . . 21. **Epistylium**
      3. Disk-segments of male flower connate into a massive ring.
         4. Leaves acuminate, neither revolute nor golden beneath, the petiole with conspicuous undulate-ruffled margins; seeds thick-walled, mottled (as in *Ricinus*); stamens 3–5. . . . . 20. **Asterandra**
         4. Leaves blunt at the tip, revolute, golden beneath, the petiole without ruffled margins; seeds thin-walled, blackened and fissured; stamens 2. . . . . 22. **Glyptothamnus** [19]
   2. Styles bifid, the branches usually slender, never lacerate (rarely adaxially auriculate).
      3. Capsule somewhat fleshy, tardily dehiscent; leaf-blades chartaceous, the blade decurrent on the petiole; stamens 3. . . . . 19. **Omphacodes**
      3. Capsule dry, promptly dehiscent; leaf-blades chartaceous to coriaceous, the blade not decurrent on the petiole; stamens 2–6.
         4. Leaf-blades small (less than 2 cm. long), with conspicuous mesophyllar sclereids, often concave beneath and with revolute margins; seeds less than 3 mm. long; stipules more or less persistent; flowers mostly appearing after the leaves. . . . . 18. **Orbicularia**

[19] Sect. **Glyptothamnus**, sect. nov. Frutices monoicae, foliis coriaceis revolutis subtus aureis; cymulis unisexualibus; flore masculo laciniis calycis 4, disco integro summopere dilatato, staminibus 2 filamentis connatis, antheris horizontaliter dehiscentibus, granis pollinis globosis areolatis; flore femineo laciniis calycis 5, disco magno integro, stylis dilatatis laceratis; seminibus fuscis sulcatis. — Species typica *Phyllanthus chryseus* Howard (sectional epithet from Gr. *glyptos*, carved, and *thamnos*, shrub, in allusion to the appearance of the massive flowers and leaves).

4. Leaf-blades larger, the sclereids aggregated within the plane, thickened marginal rim (rather than in the mesophyll); seeds over 3 mm. long; stipules caducous; flowers appearing with the leaves. ..... 17. **Thamnocharis**

1. Branchlets bipinnatiform, or modified into phylloclades.
   2. Branchlets not greatly dilated, bearing typical leaves, the penultimate axis incrustate or scurfy. ..... 23. **Hemiphyllanthus**
   2. Branchlets dilated and transformed into phylloclades, the leaves normally absent except on seedlings; axes never incrustate or scurfy. 24. **Xylophylla**

Sect. 16. **Williamia** (Baill.) Muell. Arg. Linnaea 32: 4. 1863; DC. Prodr. 15(2): 328. 1866.

Williamia Baill. Etud. Gen. Euphorb. 559, *pl. 27, figs. 9–10.* 1858.

Shrubs with phyllanthoid branching; leaves chartaceous to coriaceous, stipules deciduous or persistent. Monoecious, cymules bisexual, the flowers maturing after the leaves. Male flower: calyx-lobes 5 or 6; stamens 3–15 (very rarely 2), filaments united into a column, anthers in 1–3 whorls; pollen grains areolate. Female flower: calyx-lobes 5 or 6; disk plane, angular, often massive; ovary sessile or definitely stipitate; styles erect or spreading, free or connate, the distal ends dilated and lacerate or dentate. Capsule oblate, dry, not veiny; seeds colliculose or verruculose, less than 3 mm. long.

TYPE SPECIES: *Williamia pruinosa* Baill. (= *Phyllanthus discolor* Poepp. ex Spr.).

As here defined, the circumscription of sect. *Williamia* is enlarged from that previously held (Contr. Gray Herb. 176: 57. 1955; Jour. Arnold Arb. 37: 220. 1956) by the inclusion within it of sect. *Williamiandra*. The emended section thus comprises seven Cuban species which are indubitably related, although they are morphologically so far divergent from one another that the group might at first sight appear to be an unnatural one. A well-marked evolutionary series of increasing specialization may be traced between *P. discolor*, with its thin, unsclerified leaves and androecium of up to 15 stamens, and *P. incrustatus*, which has highly sclerified leaves and only 2–4 stamens. However, despite the prominence of these phylogenetic trends, the relationships of the species of the three subsections cannot be visualized as a simple and clear-cut "family tree."

The affinity of sect. *Williamia* with sects. *Orbicularia* and *Thamnocharis* is particularly clear in view of the fact that the latter appear to be its direct offspring. In fact, the ancestry of both sections may with reasonable confidence be traced back to subsect. *Discolores*, since *Orbicularia* and *Thamnocharis* would appear to have been derived from progenitors similar to *P. microdictyus* and *P. discolor*, respectively. In both instances differentiation of the derived taxa has involved increased foliar sclerification, but this has occurred in a strikingly different manner, for the sclereids are scattered through the mesophyll in sect. *Orbicularia*, whereas they are

aggregated within the marginal rim of the lamina in sect. *Thamnocharis*.

Because of its ancestral relationship to sects. *Orbicularia* and *Thamnocharis*, as well as the relatively unspecialized morphological features of its subsection *Discolores*, sect. *Williamia* has been placed first in the linear arrangement of sections under subg. *Xylophylla*. However, this is not intended necessarily to imply that *Williamia* is the most primitive of all the taxa within the subgenus. The differences in stamen number on which Mueller laid such stress appear far less significant in the light of present knowledge, for the stamen number of *P. discolor* is mostly 10-13 instead of the 15 reported in the literature; and in any event, even the former number is by no means a certain indication of primitiveness. The sister species of *P. discolor*, *P. microdictyus*, is more similar in floral characters to the South American sect. *Oxalistylis*. It appears that *P. discolor* and *P. microdictyus* may best be regarded as vicarious descendants from a common ancestor, specialization having progressed further in the flowers of the former and the leaves of the latter.

The flowers of *P. salviaefolius*, the type (and only?) species of sect. *Oxalistylis*, are so similar to those of *P. microdictyus*, particularly with regard to the gynoecium, that the possibility of uniting sects. *Oxalistylis* and *Williamia* might possibly be considered. However, the South American species differs by having several female flowers per cymule, differently ornamented seeds, and very different leaves much more like those of sect. *Asterandra*; so, for the time being, it seems justifiable to maintain the two sections as distinct.

KEY TO THE SUBSECTIONS AND SPECIES

1. Leaves of branchlets alternate; stigmas (style-tips) not calyptriform.
   2. Stems smooth, lenticels (if present) sparse and inconspicuous; stamens 6–15. . . . . Subsect. 16a. **Discolores**
      3. Leaves chartaceous, not highly sclerified.
         4. Calyx-lobes of female flower 2–3 mm. long; styles less than 2 mm. long; stamens mostly 9–13; leaf-blades irregularly reticulate above. . . . . 48. *P. discolor*
         4. Calyx-lobes of female flower 7–8.5 mm. long; styles 3.5–5 mm. long; stamens 6–10; leaf-blades finely and evenly reticulate above, the areoles straight-sided. . . . . 49. *P. microdictyus*
      3. Leaves coriaceous, with abundant mesophyllar sclereids. . . . . 50. *P. cristalensis*
   2. Stems incrustate, the bark breaking up into small platelets separated by spongy tissue; stamens (2–) 3–6. . . . . Subsect. 16b. **Incrustati**
      3. Stipules of branchlets acicular-conduplicate, mostly caducous; staminal column prolonged into a terminal apiculum; disk of female flower with a crenate upturned rim; leaves mostly 1.5–2.5 cm. long. . . . . 51. *P. williamioides*
      3. Stipules of branchlets nearly plane, indurate and persistent; staminal column not apiculate; disk of female flower plane, entire.
         4. Leaf-blades 2.5–4.5 cm. long, prominently reticulate beneath;

pedicel of female flower 10–15 mm. long; stamens 5 or 6. ..... 52. *P. excisus*

4. Leaf-blades 0.7–1.5 cm. long, obscurely reticulate beneath; pedicel of female flower 1–3 mm. long; stamens 3 or 4 (rarely 2). ..... 53. *P. incrustatus*

1. Leaves of branchlets opposite; stigmas (dilated style-tips) forming a cap covering most of the ovary; axes with conspicuous lenticels. ..... Subsect. 16c. **Mirifici**

Only species ..... 54. *P. mirificus*

Subsect. 16a. **Discolores,** subsect. nov.

Williamia Baill. Etud. Gen. Euphorb. 559, *pl. 27, figs. 9–10.* 1858.
Phyllanthus sect. *Williamia* (Baill.) Muell. Arg. in DC. Prodr. **15**(2): 328. 1866 (ex p.).

Stems smooth, lenticels obsolete or sparse; leaves of branchlets alternate, chartaceous or (in *P. cristalensis*) coriaceous and sclerified; stamens 6–15 (number unknown in *P. cristalensis*); styles erect, the tips moderately dilated.

TYPE SPECIES: *Phyllanthus discolor* Poepp. ex Spr.

There can be no doubt that subsect. *Discolores* occupies a significant position in the evolutionary sense, for sects. *Thamnocharis* and *Orbicularia* may with a high degree of probability be spoken of as derived from *P. discolor* and *P. microdictyus*, respectively. If, as suggested above, the high stamen number of *P. discolor* is secondarily derived from a 5- or 6-merous condition, there has at any rate been a reduction in number in the species of the derived taxa (subsect. *Incrustati*, sects. *Thamnocharis* and *Orbicularia*).

The inclusion of *P. cristalensis* within this subsection can only be provisional, for its floral characters are still insufficiently known. On the basis of its vegetative characters, it would appear to be related to *P. microdictyus* and *P. excisus*, since it has the smooth axes of the former and the highly sclerified leaves of the latter. Should its present position appear justified after the examination of adequate fertile material, *P. cristalensis* would represent a nearly schematic connecting link between subsects. *Discolores* and *Incrustati*.

48. **Phyllanthus discolor** Poepp. ex Spr. Syst. 3: 21. 1826.
(PLATE XXV, *figs.* A–C).

Phyllanthus pruinosus Poepp. ex Rich. in Sagra, Hist. Nat. Cuba **11**: 216. 1850; non sensu Muell. Arg. in DC. Prodr. **15**(2): 387. 1866.
Williamia pruinosa (Poepp.) Baill. Etud. Gen. Euphorb. 560, *pl. 27, figs. 9–10.* 1858.
Diasperus discolor ("Spr.") O. Ktze. Rev. Gen. **2**: 599. 1891.
Diasperus pruinosus ("Rich.") O. Ktze. op. cit. 600.
Phyllanthus decander Sessé & Moc. Fl. Mex. ed. 2, 212–213. 1894.

A shrub becoming c. 1–2 m. high, sparsely branching, the main stem(s)

slender (mostly 2–3 mm. thick), light brown, smooth, terete, with brown pith. Cataphylls not indurate, early deciduous: stipules triangular to lanceolate, acute or acuminate, 4–8 mm. long and 1–2 mm. broad (smaller on weak shoots), truncate at the base, thin and scarious, dark reddish brown with narrow paler denticulate or entire margins; blade linear-lanceolate, acuminate, 4–6 mm. long and 0.7–1 mm. broad. Deciduous branchlets 8–15 (–25) cm. long, 0.7–1.3 mm. thick, light brown or stramineous, terete to distinctly flattened, with (5–) 7–14 (–16) leaves; first internode 1.5–3 cm. long, median internodes mostly 1–2 cm. long. Leaves: stipules thin and scarious, early deciduous (except at tips of branchlets), linear-lanceolate, acuminate, (2.5–) 3.5–6.5 (–7) mm. long, (0.4–) 0.7–1.2 mm. broad, brownish, with entire margins. Petioles 2–4 mm. long, subterete, dark brownish, smooth. Leaf-blades chartaceous, mostly ovate or elliptic, (2–) 2.5–4 (–5.5) cm. long, (1–) 1.3–3 (–3.5) cm. broad, narrowed to an obtuse (less commonly rounded or emarginate) inconspicuously apiculate tip, acute to truncate or rarely subcordate at the base; above olivaceous or bright green, the midrib and the arching, crooked laterals slightly raised; beneath whitish- or creamy-pruinose (due to a waxy coating), the midrib salient, the laterals (c. 5–7 on a side) raised, minor veinlets forming a fine reticulum; margins unthickened, plane or casually revolute.

Monoecious; branchlets usually but not always floriferous; cymules bisexual, each most often with 1 or 2 (3) central female and c. 4–6 lateral male flowers; bracteoles of cymules triangular, dark brown, scarious, persistent.

Male flower: pedicel (1.5–) 2–6 mm. long. Calyx-lobes 5, chartaceous, subequal or usually unequal, rounded at the tip, entire or minutely denticulate near the apex; outer lobes ovate or oblong, 1.2–2.5 mm. long and 0.9–1.3 mm. broad; inner lobes obovate or spathulate, 1.7–3.5 mm. long and 1.3–1.9 mm. broad, 3- to 5-nerved from the base. Disk-segments 5, roundish, smooth and entire, c. 0.3–0.5 mm. broad. Stamens (7–) 9–13 (–15); filaments connate into a column c. 1–2 mm. high, the free portions 0.2–0.75 mm. long, erect or arching and spreading; stamens spirally arranged or in two superposed whorls with a whorl of 3 (–5) terminating the column; anthers c. 0.2–0.4 mm. long, 0.25–0.5 mm. broad, the upper erect or ascending, the lower often spreading or deflexed; anther-sacs slightly divergent, dehiscing longitudinally, the slits contiguous but usually not confluent; pollen grains 18–27 μ in diameter.

Female flower: pedicel slender, becoming (3–) 5–13 (–17) mm. long. Calyx-lobes 5, distinctly unequal, rounded at the tip, entire, with several veins from the base (at least in the larger); outer lobes ovate or oblong, 1.2–1.8 mm. long, 0.6–1.3 mm. broad; inner lobes (2–) 2.5–3 mm. long, 1.5–2.8 mm. broad. Disk rather massive, obtusely 5-angled, foveolate, the margins plane and entire. Ovary oblate or foveolate, with 3 low but distinct ribs, usually sessile; styles erect, somewhat unequal, free or connate at the base, c. 0.3–0.7 mm. long, the dilated ends (stigmas) roundish or crescent-shaped, crenulate or lacerate (but often appearing entire due

to recurved tips of lobes), sometimes adaxially auriculate, 0.5–0.8 mm. broad.

Capsule oblate, smooth or somewhat rugulose, rounded in outline, reddish brown, c. 2.1–2.3 mm. in diameter. Columella slender, 1.2–1.5 mm. long. Seeds acutely trigonous, symmetric, 1.7–1.8 mm. long, 1.1–1.3 mm. radially, 1.2–1.25 mm. tangentially, brown with somewhat irregular longitudinal lines of transversely elongate dark reddish brown dots; hilum triangular, c. 0.4 mm. long.

Collected in flower and fruit January through August.

TYPE: "Ad rivulos Cubae in Sumidero," *Poeppig* (W, LECTOTYPE; BR, F, ISOTYPES). Poeppig's material appears to include more than one collection. The lectotype collection is the one associated with the printed label reading "Phyllanthus discolor En pl. Cub. MSS. . ."; but several additional collections made in Cuba in 1823 by Poeppig (all apparently in Matanzas province) are preserved in the Vienna herbarium. A specimen in the Paris Museum bearing the label "Phyllanthus pruinosus Poepp. (ad Spreng. ad Phyll. polygonoid. Nutt. ductus) Cuba. Sylvae lucidae" and a specimen collected for Sagra (also in the Paris Museum) represent the type material of *P. pruinosus* Poepp. ex Rich.

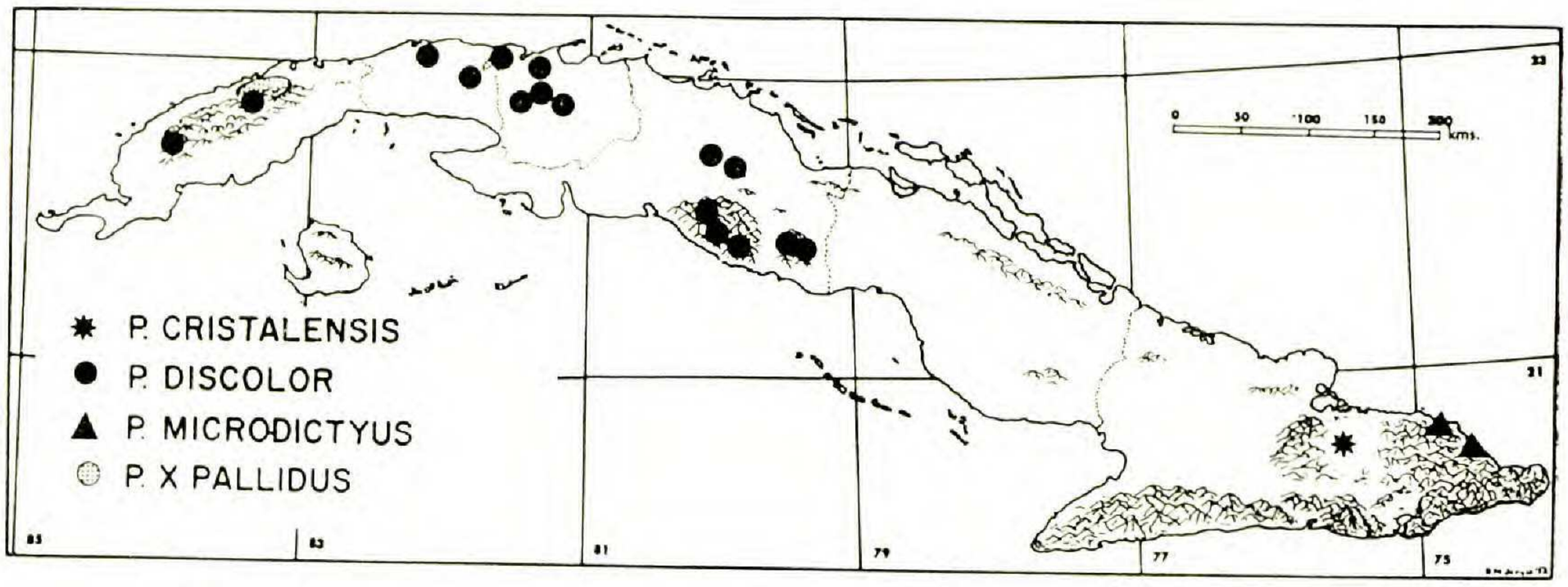
Although applied by Mueller and others to the plant known in this work as *P. caroliniensis* ssp. *saxicola*, the name *P. pruinosus* Poepp. ex Rich. is actually a synonym of *P. discolor*. Its publication was apparently inadvertent, for Poeppig's specific name, when it appears on the labels in script specially printed for his collection, is usually associated with specimens of *P. caroliniensis* ssp. *saxicola*. Evidently there was a mixture of labels in the case of the Poeppig specimens which went to Paris, so that Richard was misled into describing the present plant under a different name than that intended by Poeppig. Mueller (Linnaea 32: 30. 1863) independently published *P. pruinosus* for the other plant, as designated by Poeppig, but this name must of course be rejected as a later homonym.

DISTRIBUTION: serpentine barrens and hillsides, central and western Cuba (MAP XXII).

CUBA: without locality, *Sagra* (A,P,W: SYNTYPES of *P. pruinosus*). PINAR DEL RIO: Sumidero, between Hoyo Colorado and Francisco, at a brook, *Ekman 18205* (S); Los Organos, Sabanilla, *Wright 1941* ex p. (F, GH, GOET, MO, NY, P, S, US; data ex GH); pinelands, Loma Cajálbana, La Palma, *Alain 2362* (GH); Sagua, Bahia Honda, *Wright 1949* (G, GH, GOET; data ex GH); Rangel, Zambumbia Hill, *León 12775* (MICH, NY). HABANA: La havane, 1821, *Leman* (P); Guanabacoa [ex Flor. Mex. ed. 2], *Sessé & Mociño 4566* (F, TYPE COLLECTION of *P. decander*); eruptive rock soil, Madruga, *Britton, Britton, & Shafer 631, 690* (NY), *León 3330* (MT, NY). MATANZAS: cuabales northwest of Pan de Matanzas, southeast of Canasí, *Ekman 16469* (S); savanna, Sabanilla de la Palma, *León, Roca, & Edmund 9652* (NY); Tetas de Camarioca, serpentine barren; *Britton, Britton, & Wilson 14063* (NY); Sumidero, *Poeppig* (W, LECTOTYPE; BR, F, MO, ISOTYPES)[20]; San Miguel de los Baños, *Killip 13867* (US),

[20] This collection is also a syntype collection of *P. pruinosus*.

León & Roca 8907 (NY). LAS VILLAS: Palm barren, Santa Clara, *Britton & Cowell 10202* (NY); arroyo Ciento Viejo, 12.5 km. east of Santa Clara, *Howard 5081* (GH, MT), *Webster et al. 250* (GH); Trinidad Mountains, El Cumbre, thickets at a brook, *Ekman 13949* (S); near Pico Potrerillo, road to Aguada del Santo, open hillsides, quite common, *Ekman 13977* (S); Sierra de San Juan, Mina Carlota (southeast of Cumanayagua), alt. 300–400 m., *Howard 5663* (GH, MT, NY); Buenos Aires, *Roig & Acuña 6152* (NY); Loma de Tibisial, Sancti-



MAP XXII. Distribution of sect. *Williamia* subsect. *Discolores* in Cuba.

Spiritus Mountains, *León & Clement 6662* (NY); Lomas de Banao, *Luna 754* (NY); Lomas del Banao, Loma del Obispo, *Ekman 16282* (S), *León 1300* (NY).

Among the woody species of *Phyllanthus* in western Cuba, *P. discolor* is second only to *P. orbicularis* in abundance and frequency. As a consequence of the restriction of *P. discolor* to areas of serpentine outcrops, it occurs as a number of more or less isolated populations which exhibit a noticeable variation in leaf shape and stamen number. However, the variation within individuals is so high and the sampling of populations so inadequate (despite the rather considerable number of specimens examined) that the extent of geographical variation is difficult to assess. This inexact knowledge of the normal range of variation within the species presents a distinct hindrance in the analysis of some highly anomalous specimens from northern Pinar del Río.

These discordant collections, which all come from the Cajálbana region between La Palma and Bahia Honda, represent the plant to which the name *P. pallidus* has been applied. Grisebach (Goett. Nachr. **1865**: 168.) differentiated *P. pallidus* from *P. discolor* on the basis of its glaucous, thicker leaves and greater crowding of anthers on the staminal column, while Mueller (DC. Prodr. **15** [2]: 328. 1866) proposed to distinguish it by its fewer flowers, the female with equal calyx-lobes and shorter pedicels, and by the pale leaves with indistinct venation. However, even a superficial survey of the specimens at hand is sufficient to show that none of these characters is stable or diagnostic. Consequently, the Cajálbana population was recently (Contr. Gray Herb. **176**: 57. 1955) reduced to varietal rank under *P. discolor*; but even this disposition scarcely ap-

peared satisfactory in view of the extreme fluctuation of characters and the lack of geographical separation between the two entities.

An intensive study of a population sample taken between La Mulata and San Juan de Sagua, together with a reexamination of available herbarium specimens of *P. pallidus*, has led to the following interpretation of the situation.

Phyllanthus × pallidus Wr. ex Griseb. Goett. Nachr. **1865:** 168. 1865, pro sp. (= *P. discolor* × *P. comptus*.)

Phyllanthus sagraeanus Urb. Symb. Ant. **9:** 182. 1924.

Phyllanthus discolor var. *pallidus* (Wr. ex Griseb.) Webster, Contr. Gray Herb. **176:** 57. 1955.

CUBA. PINAR DEL RÍO: Cajálbana, Bahia Honda, *Wright 1950* (GOET, HOLOTYPE of *P. pallidus*; G, GH, ISOTYPES); Loma de Cajálbana, cuabales, *Ekman 10471* (NY, S; TYPE COLLECTION of *P. sagraeanus*); dense cuabales, eastern slope of Loma Cajálbana, *Ekman 17347* (S); orillas del arroyo, cerca de la cumbre de la Cajálbana, *León & Charles 4956* ex p. (NY); San José de Sagua to San Marcos, on serpentine rock, *Shafer 11971* (F, MO, NY, US); between La Mulata and San José de Sagua, *Webster 4652, 4653, 4654, 4657* (undistributed); Bahia Honda, dry rocky hillside, *Wilson 9417* (NY); locality questionable, *Wright 1941* ex p. (NY, P, S, US).

Some of the specimens cited have been annotated by formula rather than by the hybrid name, since they resemble *P. discolor* rather strongly and show only a subordinate influence of *P. comptus*. The type collection of *P. sagraeanus* is the most nearly intermediate, and *Wright 1950* (the type of *P. pallidus*) approaches this condition. The most striking vegetative difference between the two hybridizing species, the type of cataphyll (much more massive in *P. comptus*), is obscured in most specimens by the prevalence of *discolor* characteristics. Several collections, notably *León & Charles 4956* and *Wright 1941*, contain a mixture of *P. pallidus* and a form indistinguishable from typical *P. discolor*; in other collections there are intermediates of varying degrees.

The decision to regard the plants assigned to *P. pallidus* as hybrids between *P. discolor* and *P. comptus* has been taken after an extended analysis involving comparisons of leaf anatomy, pollen and seed fertility, and gross morphology. Anatomical studies of cleared leaves indicate that in *P. pallidus* the veinlets are c. 20–40 μ in diameter and are quite intermediate between the tenuous veinlets of *P. discolor* (mostly 10–20 μ thick) and the knobby ones of *P. comptus* (mostly 30–60 μ thick). Of even greater interest, although not entirely conclusive, are the results of a study of pollen grains taken from herbarium specimens and stained in lacto-phenol with cotton blue, which show that there is pollen sterility (though to a highly variable degree) in specimens which are transitional between *P. discolor* and *P. pallidus*, and essentially complete sterility in specimens which are morphologically good *P. pallidus*.

Since the assignment of specimens to *P. pallidus* or to the "transitional" column is somewhat arbitrary, Table II does not make sufficiently explicit

TABLE II †

POLLEN AND SEED FERTILITY

P. discolor		
Alain 2362	94	
Ekman 13977	99	(+)
Ekman 16469	10, 46	
Howard 5081	72	(+)
Howard 5563	96	(+)
Webster 250	99	(+)
P. pallidus		
Ekman 10471	—	(*)
Webster 4653–1	—	(−, *)
4654	64, 93	(−, *)
4657	28, 40	(−)
Transitional between **P. discolor** and **P. pallidus**		
Ekman 17347	99	
Shafer 11971	99	
Webster 4652–1	83	(−)
4652–2	99	(−)
4652–3	91	
4652–4	92	
4652–5	20	
4652–6	14	
4652–7	70	
4652–8	97	
4652–9	100	
4652–10	67	
4652–11	98	
4652–12	61	(−)
4653–2	86	
4653–3	*	(*)

† The figures following each collection number refer to the percentage of good pollen grains as determined by examination of 200 grains from each collection; in a few cases a second determination has been made from a different flower on the same plant. Only deeply stained grains of normal appearance have been counted as good; in doubtful instances they have been scored as defective. The plus and minus signs in parentheses refer to the production of seeds, any collection with fewer than 50% viable seed having been scored minus; lack of either symbol indicates that the degree of fertility could not be ascertained from the specimen. The asterisk denotes the production of monstrous flowers.

the important fact that the most nearly "typical" specimens of *P. pallidus* (i.e., ones such as *Ekman 10471* which are exactly intermediate between *P. discolor* and *P. comptus*) are completely sterile, only the monstrous rudiments of female flowers being produced. Other collections, exemplified by *Webster 4654* and *4657*, definitely lean toward *P. pallidus* but have more or less normal flowers which are partially fertile. In the transitional plants trending toward *P. discolor* the fertility is as variable as the morphological features. *Webster 4653–3* epitomizes the situation; it has vegetative features approaching typical *P. discolor*, but its completely monstrous flowers betray its reproductive instability.

The absence of collections intermediate between *P. pallidus* and the other presumed parent species *P. comptus* may appear strange, but is perhaps explained (at least in part) by the apparent rarity of the latter, which has been collected only three times. However, if this explanation is correct it raises the even knottier problem of why the hybrid form should be so much commoner than one of its parents, particularly since it appears to become fertile only when back-crossed to *P. discolor*. Possibly some ecological factor plays an important role in determining the peculiar character of the population.

The prevalence of "pallidus" characters in the Cajálbana population of *P. discolor* might be adduced as an instance of "introgressive hybridization," although it is not evident that any characters of *P. comptus* have been diffused into any populations of *P. discolor* outside of the Cajálbana area. Much more striking than any leakage of characters is the exaggerated variability of the local population as a whole; a considerable number of specimens show anomalous characteristics. An outstanding example of this is *Ekman 10433*, which vegetatively can scarcely be distinguished from typical *P. discolor* and which has highly fertile pollen; but its flowers are exceptional in the long staminal column and styles and the stipitate ovary. These peculiarities, especially the stipitate ovary, suggest a resemblance to the related species *P. microdictyus*, which is known only from Oriente province. However, it appears probable that these unusual features have some connection with the local hybridity and do not really signify any relationship to the species of Oriente.

The enhanced degree of variability is particularly marked in the stamen number, as shown in Table III. Since *P. comptus* usually has only 5 or 6 stamens, one would expect that its hybrids with *P. discolor* might have a number approaching the usual 9–13 of the latter. Insofar as the lower numbers (under 10) are concerned, this is reasonably well borne out. But the occurrence in *P. pallidus* of numbers much higher than those in *P. discolor* is entirely unexpected. Although the number of androecia counted (50 each of *P. discolor* and *P. pallidus*) is unfortunately small, there can be little doubt that mere chance cannot account for 11 of the *pallidus* flowers having a higher number than any of the *discolor* ones.

It seems quite likely that this wholly anomalous increase in stamen number in *P. pallidus* is the result of the same cause which determined the formation of a stipitate ovary in *Ekman 10433*, i.e., the morphogenetic disturbance in the hybrid plant which is presumably due to imbalance between the chromosome complements of the parents. It is conceivable that the situation in *P. pallidus* presents us with an insight into one mechanism of phylogenetic change, for if aberrant plants of *P. pallidus* with androecia of 16–18 anthers should happen to be selected out as a separate fertile population, a new species characterized by higher stamen number might result. Possibly the prevalent numbers (9–13) in *P. discolor* arose in this same way, for the primitive number in the genus is certainly 5 or 6 as in subg. *Kirganelia*; and since *P. discolor* has no other particularly primitive characters, it is probable that its increased stamen number, too, is derived.

The relationships of *P. discolor* are reasonably well-defined, for on purely morphological grounds its affinity to the following species, *P. microdictyus*, is apparent; and the general resemblance (though much less close) to *P. comptus* supports the evidence (from the existence of *P. pallidus*) that *P. discolor* can cross with that species. Furthermore, *P. comptus* in its morphological details is transitional between *P. discolor* and the other species of sect. *Thamnocharis*, so that it presumably has evolved from *P. discolor* or some common ancestor. The hybridization occurring today

TABLE III *

VARIATION IN STAMEN NUMBER IN *P. discolor* AND *P. pallidus*

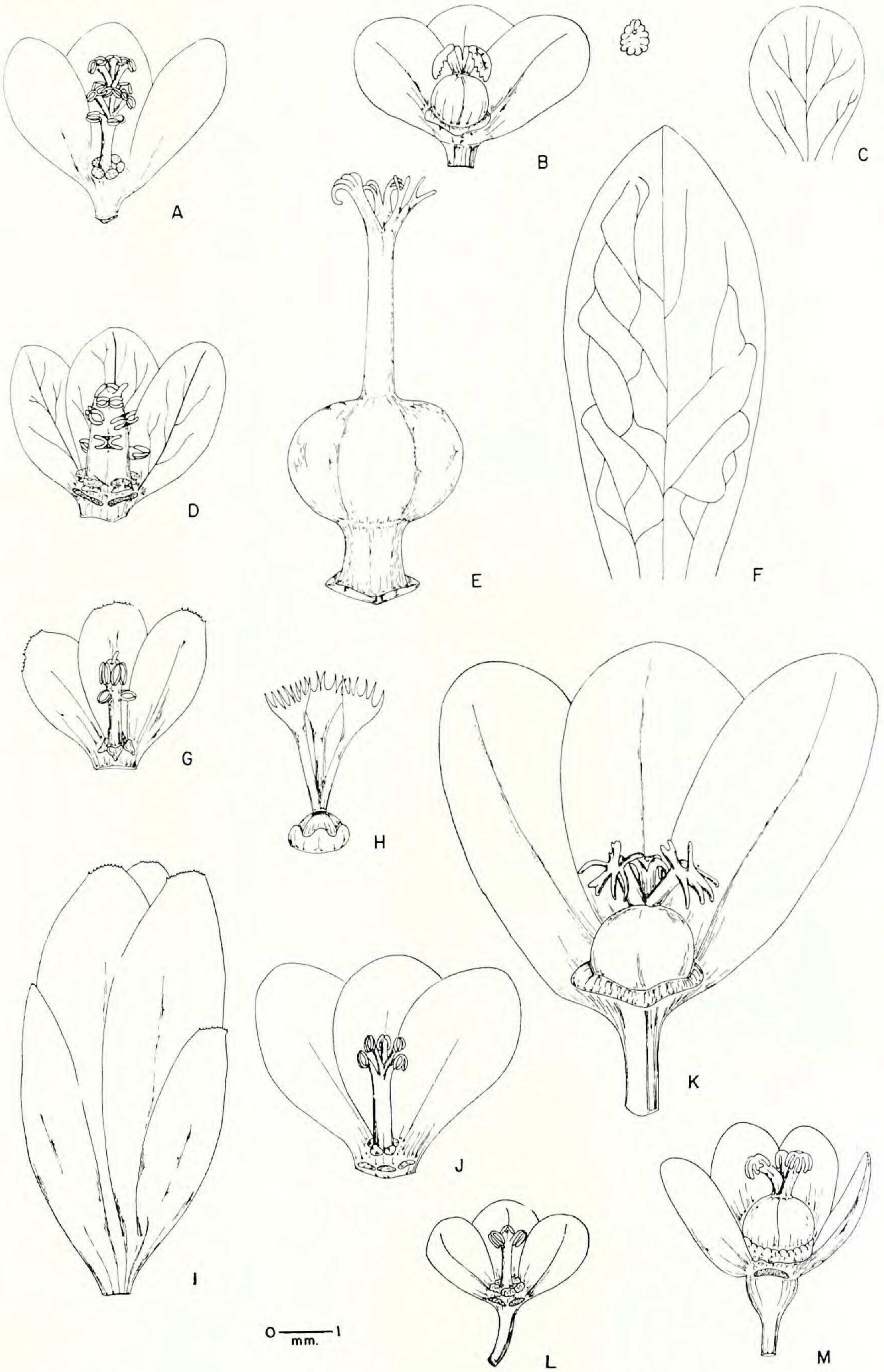
Stamen number	*P. discolor*	*P. pallidus*
18	0	1
17	0	2
16	0	2
15	0	6
14	1	4
13	12	6
12	17	7
11	6	9
10	8	5
9	4	1
8	1	4
7	1	1
6	0	1

* The figures in the two right-hand columns refer to the number of flowers having the specific stamen number. The mean number of flowers scored per collection was about 3, but there was some variation due to differences in the number of available male flowers on the specimens; this inequality in sampling may be partially counteracted by the considerable spread of variation on each plant (e.g., from 9–14 in one individual of *P. discolor*). It should be noted that the *P. pallidus* column includes collections of various transitional forms, or in other words all specimens from the Cajálbana area which are not obviously "good" *P. discolor*.

must be due to comparatively recent changes in the distribution of one or both species and, most probably, to a spread of *P. discolor* into the restricted range of *P. comptus*. It is interesting that there is no evidence of crossing between *P. discolor* and *P. orbicularis* of sect. *Orbicularia*, although the latter is also present near almost every station of *P. discolor* and shows an affinity (via *P. microdictyus*) evident enough so that crossing would *a priori* not appear impossible. Presumably there is a much stronger genetic barrier between *P. discolor* and *P. orbicularis* than between the former and *P. comptus*; this offers an interesting subject for further analysis on cytological lines.

PLATE XXV. FLOWERS OF SECT. *Williamia*, SUBSECTS. *Discolores* AND *Incrustati*.

FIGS. A–C. Male flower, female flower, and female calyx-lobe of *Phyllanthus discolor* Poepp. ex Spr. (*Webster et al. 250* [GH]). FIGS. D–F. Male flower, gynoecium, and female calyx-lobe of *Phyllanthus microdictyus* Urb. (*Marie-Victorin & Clement 21525* [A]). FIGS. G–I. Male flower, gynoecium, and female calyx of *Phyllanthus williamioides* Griseb. (*Webster 4014* [GH]). FIGS. J–K. Male and female flowers of *Phyllanthus excisus* Urb. (*Ekman 4055* [S]). FIGS. L–M. Male and female flowers of *Phyllanthus incrustatus* Urb. (*Ekman 3848* [S]).



WEBSTER, WEST INDIAN PHYLLANTHUS

49. **Phyllanthus microdictyus** Urb. Symb. Ant. 9: 183. 1924. (PLATE XXV, *figs.* D–F; PLATE XXVII, *fig.* A).

A shrub c. 1 m. high with the habit of a miniature tree, the stem simple or sparsely branching near the top; bark smooth, dark brownish, becoming finely fissured on old stems but not breaking up into plates. Cataphylls deciduous: stipules triangular-lanceolate, mostly 3–4 mm. long and (1.1–) 1.5–1.7 mm. broad (smaller on weak shoots), acute, truncate at the thickened base, lightly keeled, dark brown and scarious-indurate; blade narrowly lanceolate, acuminate, c. 2.5–3 mm. long. Branchlets (6–) 9–17 (–19) cm. long, 0.9–1.5 mm. thick, brownish, smooth and pruinose, usually flattened, with (6–) 8–12 (–14) leaves; first internode (15–) 20–40 (–45) mm. long, median internodes c. 10–20 mm. long. Leaves: stipules linear-lanceolate, acuminate, (1.5–) 2.5–3 mm. long, 0.4–1 mm. broad, scarious, deciduous. Petiole 2.5–4.5 mm. long, subterete, brownish. Leaf-blades flexibly chartaceous, ovate or elliptic, (1.5–) 2.5–5 (–6.5) cm. long, (1.3–) 2–3.5 (–4) cm. broad, emarginate (or less commonly obtuse or rounded) and minutely and inconspicuously apiculate at the tip, mostly rounded to cordate at the base; above dull green (bright red when first expanded), minutely foveolate, the midrib incised, the main laterals raised, repeatedly branching and anastomosing to form a fine raised reticulum with straight-sided meshes; beneath greyish-pruinose, the midrib raised, the laterals (c. 4 or 5 on a side) and ultimate veinlets very slightly raised, pale, forming a fine and inconspicuous reticulum; margins plane, not thickened.

Monoecious; usually the proximal 2 or 3 nodes of a branchlet with male cymules of 1–3 flowers, the succeeding nodes with bisexual cymules of 1 central female and 1 or 2 lateral male flowers.

Male flower: pedicel capillary, (5–) 7–15 mm. long. Calyx greenish white, sometimes pinkish tinged: calyx-lobes 6 (rarely 5), chartaceous, subequal, oblong to obovate, 2.5–3.5 mm. long, 1.3–2.3 mm. broad, entire and rounded at the tip, faintly triplinerved or the midrib pinnately branched. Disk-segments 6 (rarely 5), round or trigonous, smooth and entire, c. 0.25–0.45 mm. broad. Stamens 6–10 (–11), the filaments 1–1.7 mm. long, connate into a rather stout column; anthers subsessile (the free portion of the filament no longer than the anther) or the terminal ones short-stalked, inserted on the column spirally or in 2 or 3 whorls, ascending or spreading, c. 0.25–0.3 mm. long, 0.4–0.5 mm. broad; anther-sacs more or less divergent, globose before anthesis, dehiscing horizontally or obliquely, the slits apically contiguous but not confluent; pollen grains 20–24 μ in diameter, with c. 7 or 8 areoles per amb.

Female flower: pedicel capillary, (5–) 7–12 (–14) mm. long. Calyx colored as in the male; calyx-lobes 6 (rarely 7), strongly convex, subequal or unequal (the outer one or two lobes often manifestly shorter than the innermost), oblong to obovate, the larger lobes 7–8.5 mm. long, 3.5–5 mm. broad, entire and obtuse or rounded at the apex, 3–5-nerved from the base, the laterals ascending and anastomosing in a rather conspicuous net. Disk 5-angled, fairly massive in the bud but becoming fused with

and incorporated into the massive gynophore. Ovary oblate-spheroidal, about as high as (or somewhat higher than) the gynophore, pruinose; styles erect, (3.5–) 4–5 mm. high, connate ½ to ¾ their length, gradually dilated at their ends into conspicuously lacerate 3- or 4-parted tips.

Capsule oblate, emarginate at the apex, c. 5 mm. in diameter, smooth, reddish brown, held within the erect appressed calyx-lobes. Columella conical, somewhat constricted at the tip, 2.2–2.4 mm. long. Seeds [those examined not quite mature] plano-convex, 2.5–2.7 mm. long, 1.5–1.6 mm. radially and tangentially, dark shiny reddish brown, nearly smooth (minutely colliculose); hilum submedian, triangular, light brown.

Flowering and fruiting April through July and possibly later, but apparently sterile during the winter.

TYPE: Cuba, *Ekman 3705*.

DISTRIBUTION: lowlands near the coast, northeastern Oriente Province, Cuba (MAP XXII).

CUBA. ORIENTE: Moa region, Cayoguan, *Acuña 12478* (SV [Herb. Roig n. 8593], US); Mina Cromita, Cayoguan, south of Punta Gorda, *Clemente & Alain 4074* (MICH); Rio Cayoguan, près du pont sur le chemin de la mine Delta, *Marie-Victorin & Clement 21525* (A, MT), *21749* (MT); same locality, cut-over forest of *Clusia*, *Bactris*, *Arthrostylidium*, *et al.*, *Webster 3809* (GH, MICH); ad Taco Bay prope Baracoa in pinetis, 2 December 1914, *Ekman 3705* (S, HOLOTYPE; NY, ISOTYPE fragment and photograph; sterile).

A very distinctive and well-marked species, *P. microdictyus* appears to be quite restricted in range; the first four collections cited are all essentially from the same locality, so that there are, in effect, only two known stations. Although Ekman's type specimen is sterile, the characteristic venation of the leaves — identical with that of the fertile collections from Moa — leaves no doubt as to the identity or typification of the species. Ekman's designation of the Taco Bay collection as being from pinelands suggests a somewhat different habitat from the flood-plain woods along the Río Cayoguan, but the species would in any case appear to be a relatively mesophytic one.

Because of their evolutionary significance, the several affinities of *P. microdictyus* deserve special mention. Its large female flowers with long styles and stipitate ovary are so similar to those of the South American *P. salviaefolius* that there can be little doubt of a fairly close relationship, although the latter species differs vegetatively by having hirsutulous axes and acuminate, more coarsely veined leaves. However, *P. microdictyus* is also an obviously near relation of *P. discolor,* which it greatly resembles vegetatively. Furthermore, the incipient production of mesophyllar sclereids in *P. microdictyus* presages their full development in *P. cristalensis*; and since it would appear that it is through the latter (or a similar species) that the highly specialized representatives of subsect. *Incrustati* and sect. *Orbicularia* have originated, it would not be incorrect to regard *P. microdictyus* as the progenitor of this entire phylogenetic line.

50. **Phyllanthus cristalensis** Urb. Repert. Sp. Nov. **28**: 212–213. 1930.

Glabrous shrub up to 1.5 m. high; branches shiny reddish brown, becoming grey with age, c. 1.5–3 mm. thick. Cataphylls black, indurate, soon deciduous: stipules lanceolate, c. 1.5–2 mm. long, acuminate, entire; blade narrower. Branchlets mostly 4–11 cm. long, 0.5–0.8 mm. thick, smooth, reddish brown, subterete (slightly compressed proximally), with 8–15 leaves; first internode c. 5–15 mm. long, median internodes 4–7 mm. long. Leaves: stipules reflexed, subpersistent, triangular-lanceolate, 1.7–2 mm. long, 0.7–1.1 mm. broad, rather blunt at the tip, entire, dark brown, somewhat indurate. Petiole 1.5–2.5 mm. long, slightly flattened, dark brown, nearly smooth. Leaf-blades coriaceous, broadly elliptic to suborbicular, c. 1–2.2 cm. long, 0.8–1.9 cm. broad, emarginate and with a deciduous apiculum at the tip, rounded to emarginate at the base; above dull brownish olivaceous, mottled (the cell outlines of the irregularly anastomosing veins visible under a lens), the subprominent midrib plane or sunken, the laterals rather obscure; beneath greyish or brownish, the midrib and laterals (c. 4 or 5 on a side) plane, not very prominent, the reticulum obscure; margins plane, scarcely thickened.

Monoecious (presumably); flowers [and fruit not seen, description ex Urban] few, solitary or paired, pedicels 3–5 mm. long.

Male flower: calyx-lobes 5, narrowly ovate, 2 mm. long, barely 1 mm. broad; stamen number not determined; filaments connate, anthers discrete. Female flower: pedicel narrowly obconic-thickened above; calyx-lobes 5, narrowly ovate, 2 mm. long; styles not seen.

Capsule oblate, rounded-trigonous, c. 4 mm. in diameter; seeds brownish, minutely puncticulate, c. 2 mm. long, 1.7 mm. broad.

TYPE: Cuba, *Ekman 15993*.

DISTRIBUTION: endemic to the Sierra Cristal, eastern Cuba (MAP XXII).

CUBA. ORIENTE, Sierra Cristal: at the tributary of the Río Lebisa in charrascales, alt. 600–1100 m., 15 Dec. 1922, *Ekman 15967* (S); in low *Arthrostylidium* thickets which cover the top, alt. 1100–1325 m., 15 Dec. 1928, *Ekman 15993* (NY, ISOTYPE); ridge west of Pico Cristal, mossy elfin forest, 4 Mar. 1954, *Jervis 3206* (GH).

Although still poorly known, *P. cristalensis* is evidently a very distinct species on the basis of its vegetative characters. Vegetatively it is intermediate between subsects. *Discolores* and *Incrustati*, having the smooth axes of the former combined with the highly sclerified leaves of the latter. However, until adequate flowering material can be collected its relationships cannot be satisfactorily determined.

Subsect. 16b. **Incrustati**, subsect. nov.

Phyllanthus sect. *Williamiandra* Griseb. Goett. Nachr. **1865**: 171. 1865.
Ramsdenia Britton, Mem. Torr. Bot. Club **16**(2): 72. 1920.

Stems and branchlets incrustate with dark bran-like flakes of bark:

leaves of branchlets alternate, coriaceous (heavily sclerified within); stamens (2–) 3–6; styles erect, conspicuously lacerate.

TYPE SPECIES: *Phyllanthus williamioides* Griseb.

Grisebach proposed to distinguish sect. *Williamiandra* on the basis of its androecium and styles, but his description of the androecium is erroneous and his discussion misleading. The type species, *P. williamioides*, has only 5 or 6 stamens (not 10 as reported by Grisebach), and the conical apex of the staminal column cannot serve as a sectional character since it does not occur in the two related species. Grisebach's stated distinction between the styles of *Williamiandra* (correctly likened to those of sect. *Oxalistylis*) and those of sect. *Williamia* is wholly incorrect, for he erroneously describes the styles of the latter as bifid. Except for the difference in stamen number, there are no floral characters available for separating *Williamia* from *Williamiandra*; but since the species of the two groups can be distinguished vegetatively, it seems appropriate to place them into two subsections of the inclusive sect. *Williamia*.

Britton's proposed genus *Ramsdenia,* which included *P. excisus* and *P. incrustatus*, corresponds almost exactly to the present subsection; he did not discuss its relationships or clearly define its characters, and he was apparently unaware of the existence of *P. williamioides*.

51. **Phyllanthus williamioides** Griseb. Goett. Nachr. **1865**: 169–170. 1865; Muell, Arg. in DC. Prodr. **15**(2): 328–329. 1866.
(PLATE XXV, *figs.* G–I).

Diasperus williamioides (Griseb.) O. Ktze. Rev. Gen. **2**: 601. 1891.

A small shrub 0.5–1.5 (–2) m. high, with two or more stems clustered on a gnarled caudex (stem unbranched in young plants); bark of stem-base and root broken up into conspicuous patterns of squares. Stems and branchlets incrustate but the bark-platelets smooth and glabrous, dark brown, the exposed spongy tissue reddish brown. Cataphylls blackish, indurate but mostly soon deciduous: stipules lanceolate, (1.5–) 1.8–2.7 mm. long, 0.7–1.2 mm. broad; blade c. 1.8–2.5 mm. long, 0.5 mm. broad. Branchlets erect or spreading, (5–) 8–15 (–19) cm. long, 1–1.2 mm. thick, reddish-brown- or blackish-incrustate, terete or angled, with mostly 10–25 (–35) leaves; first internode (5–) 7–12 (–16) mm. long, median internodes 2–6 (–10) mm. long. Leaves: stipules acicular-lanceolate (convexly conduplicate), soon deciduous, 2.5–3.5 (–5) mm. long and 0.5–1 mm. broad, rather blunt at the tip, chartaceous, dark brown. Petiole 1.5–2.5 mm. long, brownish, smooth, flattened. Leaf-blades coriaceous, mostly orbicular or nearly so (sometimes slightly obovate or broader than long), (1–) 1.5–2.5 cm. long, (1–) 1.3–2.2 cm. broad, retuse or emarginate at the tip, cordate at the base; above olivaceous and sublucid or dully plumbeous, minutely foveolate-reticulate, the midrib slightly incised, the lateral veins and veinlets forming a fine slightly raised reticulum; beneath brownish- or olivaceous-plumbeous (minutely white-dotted with wax-covered stomata), the midrib plane, the slightly raised laterals (c. 5 or 6 on a side) anas-

tomosing with the conspicuous tertiary veinlets to form a close reticulum; margins plane, not thickened.

Monoecious, flowers in axillary bisexual cymules; central flower female, lateral ones male (the male mostly developing after fruiting calyx has fallen, so that the arrangement on the branchlet appears to be of proximal racemes of male flowers and distal solitary female flowers); bracteoles blackish and indurate.

Male flower: pedicel c. 1.8–2 mm. long. Calyx greenish white, whitish, or reddish tinged; calyx-lobes 5, thin but coriaceous, subequal, oblong to spathulate, (1.3–) 1.5–2.3 mm. long, 0.7–1.5 mm. broad, denticulate near the apex, more or less triplinerved but nerves rather obscure. Disk-segments 5, flattened or concave, roundish or triangular, smooth and entire, 0.25–0.35 mm. broad. Stamens 5 or 6, the filaments connate into a relatively slender column 1–1.1 mm. high and 0.25–0.4 mm. thick; anthers in two series, the upper of 3, the lower of 2 or 3, the apex of the column terminated by an apiculum; anthers slightly apiculate, sessile on the column or very nearly so, the upper erect, the lower ascending or spreading, c. 0.3–0.4 mm. long and broad; anther-sacs sub-parallel, dehiscing longitudinally, the slits not confluent; pollen grains 24–27 μ in diameter, the areoles polybrochate, c. 5–6 μ across, c. 10 per amb.

Female flower: pedicel short and stout, only (0.7–) 1.2–1.8 (–2.4) mm. long. Calyx colored as in the male; calyx-lobes 5–7, quite unequal, denticulate at the apex, incrassate at the base, nerves several but obscure; outer lobes oblong, obtuse, 2.5–3.5 mm. long, 1.5–2 mm. broad; inner lobes obovate, rounded at the tip, 5–5.5 mm. long, 2.2–2.8 mm. broad. Disk a thick brownish crenate-rimmed cup, enclosing the base of the ovary. Ovary sessile, smooth, carinate between the septae; styles erect, free, 1.8–2.7 mm. high, the dilated tips more or less 3-fid, the three branches with a total of c. 8–10 slender lacerae.

Capsule subglobose, c. 4 mm. in diameter, the valves olivaceous, smooth, not veiny, 3.5 mm. long, often retained within the appressed calyx-lobes. Columella 2.2 mm. long. Seeds trigonous, somewhat asymmetric (excentrically carinate on the back), 2.2–2.3 mm. long, 1.2–1.5 mm., radially and tangentially, blackish brown, colliculose on back and sides; hilum subterminal, elliptic or ovate, c. 0.5 mm. long.

TYPE: Cuba, *Wright 1944*.

DISTRIBUTION: endemic to the Baracoa region, Oriente province, Cuba (MAP XXIII).

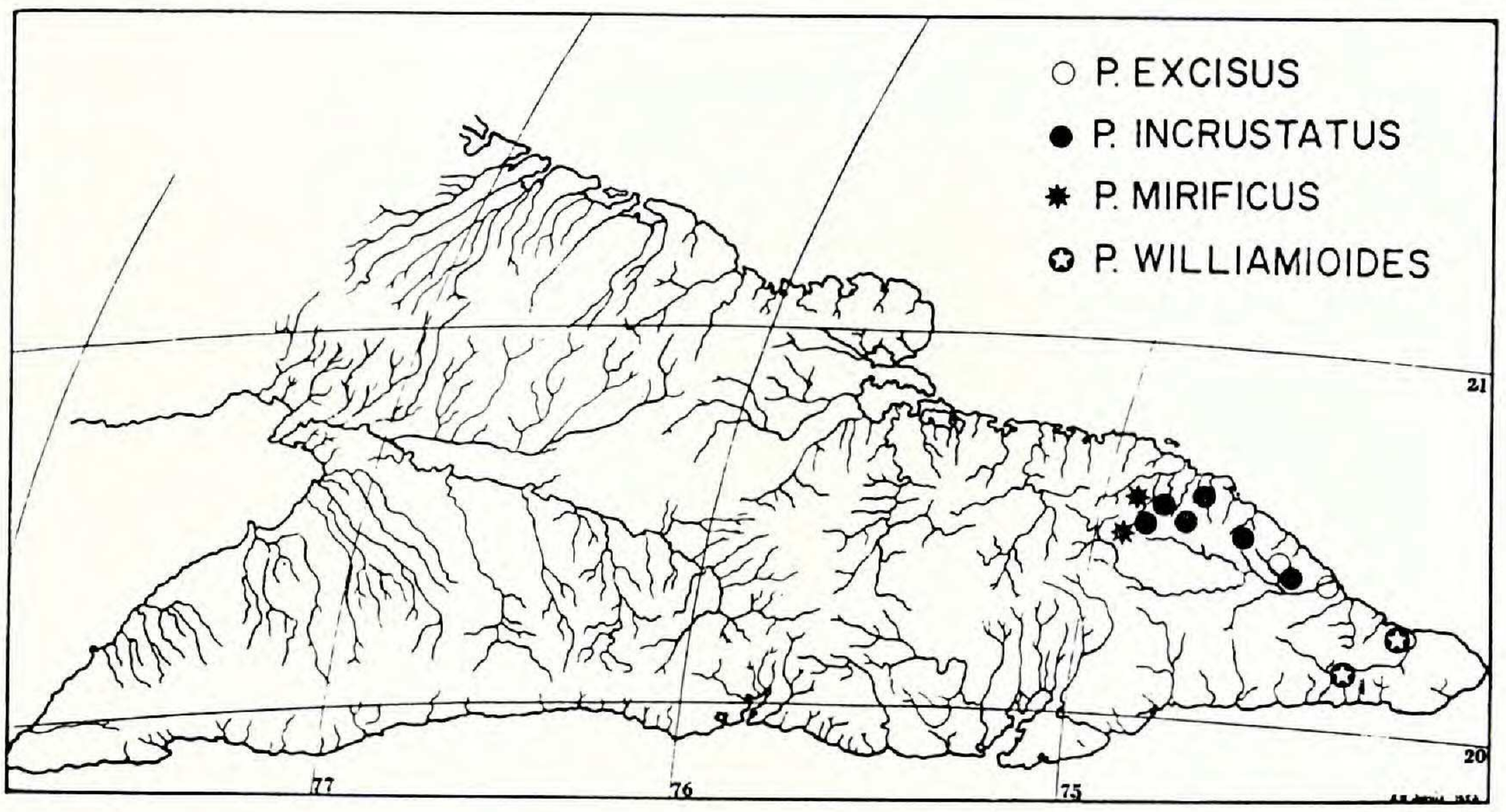
CUBA. ORIENTE: Cuchillas de Baracoa, *Wright 1944* (GOET, HOLOTYPE; GH, ISOTYPE; locality ex isotype); Altos de Farola, c. 20 miles south of Baracoa, pineland at 1750 ft., 3 Aug. 1951, *Webster 4014* (GH, MICH, NY); among pines and tree ferns, moist arroyo c. 12 miles east of Baracoa, 18 Mar. 1954, *Jervis 3332* (GH).

Wright's type collection differs from the other specimens in its distinctly obovate leaves. However, in the field, leaves of this shape were found on shoots from the base of plants which higher up bore orbicular leaves; it

thus appears that Wright made his collection from a stump sprout or very depauperate plant.

The present species is very closely related to *P. incrustatus*, but is usually distinguishable at first sight by virtue of its smooth bark platelets (these usually scabridulous in *P. incrustatus*) and larger more elongated leaves. Actually, the concave deciduous stipules and androecium of 5–6 stamens are the best diagnostic features of *P. williamioides*, and will always permit its ready separation from *P. incrustatus*.

As in many species of subg. *Xylophylla*, the leaves of *P. williamioides* are distinctly reddish-tinged when young, though less strikingly so than in *P. pachystylus*. The undersurface is pale yellow at first and only later becomes green; this behavior, again, is characteristic of many other species.



MAP XXIII. Distribution of sect. *Williamia* subsects. *Incrustati* and *Mirifici* in eastern Cuba.

52. **Phyllanthus excisus** Urb. Repert. Sp. Nov. 13: 449–450. 1914. (PLATE XXV, *figs.* J–K).

Ramsdenia excisa (Urb.) Britton, Mem. Torr. Bot. Club 16(2): 72. 1920.

Shrub c. 2–3 m. high; pith brownish; stems and branchlets incrustate with smooth dark reddish brown platelets, the interspaces of spongy tissue light reddish brown. Cataphylls blackened, indurate, more or less persistent: stipules triangular-lanceolate, 2–2.5 mm. long, 1.5–1.6 mm. broad, acuminate; blade narrower. Branchlets stout, 9–27 cm. long, 1.7–3 mm. thick, reddish brown and incrustate, subterete (more or less angled distally), with (10–) 15–35 nodes; first internode (5–) 10–15 (–20) mm. long, median internodes 5–18 mm. long. Leaves: stipules lanceolate, 2.5–3 mm. long, 1.1–1.5 mm. broad, acuminate, quite oblique at the base, blackish, indurate, appressed or spreading, persistent. Petioles 1.5–3 mm. long, brownish, transversely furrowed, with a deep median adaxial groove.

Leaf blades coriaceous, mostly ovate or elliptic, (2.5–) 3–4.5 cm. long, 2.5–3.5 cm. broad, emarginate at the tip, obtuse to subcordate at the base; above olivaceous-plumbeous, minutely foveolate-reticulate, the midrib plane or slightly impressed, the lateral veins obscure; beneath brownish grey when dried (not white-dotted), the midrib saliently raised, the laterals (c. 6–8 on a side) and tertiary veinlets slightly raised, anastomosing to form a rather prominent reticulum; margins unthickened, plane.

Monoecious; flowers in axillary bisexual cymules, each of a solitary central female flower and a few (c. 3 or 4) male flowers on bracteolate lateral axes; bracteoles indurate, persistent in old axils.

Male flower: pedicel capillary, c. 4–5.5 mm. long. Calyx whitish (ex Shafer); calyx-lobes 5, subequal, oblong to obovate, (3–) 3.3–4 mm. long, 1.5–2 mm. broad, entire, the venation obscure. Disk-segments 5, roundish, entire, c. 0.4–0.5 mm. across. Stamens 5–6, filaments united into a rather stout non-apiculate column 1.5–1.8 mm. high and 0.5–0.6 mm. broad; anthers biseriate (upper series of 3, lower of 2 or 3) but both whorls crowded at the top, not evidently apiculate; anther-sacs subparallel, dehiscing longitudinally, the slits not confluent; pollen grains 19–22 μ in diameter, the areoles polybrochate, c. 7–11 μ long, 4–5 per amb.

Female flower: pedicel nearly straight, slender, (10–) 12–15 mm. long. Calyx greenish-white (ex Shafer); calyx-lobes 5, coriaceous, thickened at the base, subequal (the outer slightly narrower), oblong to obovate, the larger lobes 5–7 mm. long [up to 8 mm., ex Urb.], 2.5–4.5 mm. broad, entire and rounded at the tip, the venation obscure. Disk massive, obtusely 5-angled, entire (or minutely crenulate), obscurely foveolate, the margin plane, somewhat thinner. Ovary sessile, carinate dorsally; styles erect, free or shortly connate at the base, 1.8–2 mm. high, the dilated ends deeply parted into 6–7 (–10) narrow divaricate lacerae; outline of stylar apex roughly triangular, two arms extending adaxially, the third abaxial and with more lobes.

Capsule subglobose, emarginate, c. 5 mm. in diameter, smooth or slightly rugulose, brownish, not veiny. Columella c. 3 mm. long. Seeds [seen only in immature condition] c. 3 mm. long, brownish, probably with the ornamentation of *P. williamioides* when mature.

TYPE: Cuba, *Shafer 4447*.

DISTRIBUTION: endemic to the Baracoa region, Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Navas to Camp Buena Vista, alt. 650 m., 23 March 1910, *Shafer 4447* (NY, LECTOTYPE; F, MO, US, ISOTYPES); prope Baracoa, ad Maraví in pinetis, 26 Dec. 1914, *Ekman 4055* (S).

Apparently a rare species of restricted range, *P. excisus* is well distinguished from the two related species of subsect. *Incrustati* by its larger ovate leaves, larger flowers on longer pedicels, and different styles. Its

strong resemblance to *P. microdictyus* of subsect. *Discolores* can hardly be mere coincidence, and it can be rather confidently regarded as a xerophytic derivative of that plant. The flowers of both species are similar, but *P. excisus* has fewer stamens and, of course, its incrustate stems and coriaceous leaves easily separate it from *P. microdictyus*.

The apparent rarity of *P. excisus*, as compared with the other Oriente species of sect. *Williamia*, may prove to be illusory, for the region between Navas and Baracoa has been much less visited by collectors than the Moa district, which up until recently was much more accessible.

53. **Phyllanthus incrustatus** Urb. Repert. Sp. Nov. **13**: 449. 1914. (PLATE XXV, *figs.* L–M).

Ramsdenia incrustata (Urb.) Britton, Mem. Torr. Bot. Club **16**(2): 73. 1920.

Shrub 0.5–2 m. high; stems and branchlets usually scabridulous-hirtellous at the tips, below incrustate with scabridulous platelets of bark (rarely the platelets smooth). Cataphylls blackish, indurate, subpersistent: stipules triangular to narrowly lanceolate, (1–) 1.5–3.7 mm. long, 0.5–1 mm. broad, acute to acuminate (sometimes with very attenuate tips), sometimes excentrically keeled, becoming reflexed or spreading; blade narrowly lanceolate, (0.7–) 1.5–3.5 (–5) mm. long, also more or less reflexed. Branchlets (5–) 7–17 (–26) cm. long, 1–1.7 mm. thick, incrustate with dark brown usually scabridulous platelets separated by lighter reddish brown furrows, with (10–) 15–40 (–60) leaves; first internode 3–10 mm. long, median internodes 2–6 mm. long. Leaves: stipules persistent, appressed or reflexed, triangular to linear-lanceolate, (0.8–) 1.2–2.5 (–3.2) mm. long, 0.3–0.9 mm. broad, acute or acuminate, dark brown, more or less indurate. Petiole 1–1.8 mm. long. Leaf blades coriaceous, mostly orbicular or suborbicular (sometimes broader than long), c. 7–12 (–15) mm. long, 6–12 (–14) mm. broad, usually retuse or emarginate and inconspicuously apiculate, truncate or more commonly cordate at the base; above dull olivaceous or plumbeous, minutely foveolate-reticulate, the midrib impressed, the laterals usually rather obscure; beneath greyish brown or purplish brown (minutely white-dotted with wax-covered stomata), the slightly raised laterals (c. 5 or 6 on a side) anastomosing with the veinlets to form an inconspicuous reticulum; margins plane, not thickened.

Monoecious; flowers in axillary bisexual cymules; first (central) flower of cymule female, rapidly maturing and deciduous, succeeded by several male flowers on one or both lateral abbreviated axes; branchlets thus appearing (as in *P. williamioides*) to have short racemes of male flowers at proximal nodes and solitary female flowers at distal nodes.

Male flower: pedicel (0.5–) 1–1.5 mm. long. Calyx whitish (in living condition [ex Shafer], reddish when dried); calyx-lobes 5, subcoriaceous but thin, subequal, oblong to obovate or spathulate, (1.3–) 1.5–2.4 mm. long, (0.7) 1–1.5 mm. broad, rounded at the tip, entire or occasionally denticulate, nervation obscure, only the midrib at all prominent. Disk-

segments 5, flattened or concave, roundish or trigonous, c. 0.25–0.35 mm. across. Stamens 3 or 4 (rarely 2), filaments connate into a slender non-apiculate column 0.6–1.2 mm. high and 0.15–0.25 mm. thick; anthers sessile, aggregated into a mass at the top of the column, 0.25–0.35 mm. long; anthers-sacs parallel, dehiscing longitudinally and vertically, the slits not confluent; pollen grains 12–19 μ in diameter, the areoles polybrochate, c. 6–7.5 μ long, c. 3–5 per amb.

Female flower: pedicel slender or incrassate above the middle, 1–3 mm. long. Calyx colored more or less as in the male; calyx-lobes 5, rather unequal, rounded at the tip, entire, the outer oblong, 1.6–2.7 mm. long and 0.8–2.3 mm. broad, the inner mostly spathulate or obovate, 1.8–3.3 mm. long and 1.2–3.3 mm. broad; nervation obscure. Disk massive, 5-angled, entire, plane, foveolate. Ovary sessile; styles free or shortly connate below, spreading or ascending, flattened, 0.5–0.6 mm. long, the dilated apices 5–6-lacerate.

Capsule subglobose, emarginate, c. 3–4.5 mm. in diameter, the valves smooth, dark brown, not veiny. Columella 1.5–2 (–2.5) mm. long. Seeds trigonous, asymmetrically carinate on the back, 1.8–2.7 mm. long, 1.1–1.8 mm. radially, 1.35–1.45 mm. tangentially, reddish brown, nearly smooth.

TYPE: Cuba, *Shafer 4020* (NY, LECTOTYPE; the original specimen of this collection in Herb. Krug & Urban destroyed during World War II).

DISTRIBUTION: wooded areas, northeastern Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Cumbre Cayo [Cayoguan], *Acuña 12477* (US); Mina Delta, c. 500 m. alt., échine de serpentine sur le chemin de la mine Delta, *Marie-Victorin & Clément 21754* (A, MT); Camp La Gloria, south of Sierra Moa, *Shafer 8113* (F, MO, NY, US); damp thickets between Río Yamaniguey and Camp Toa, alt. 400 m., 22–26 Feb. 1910, *Shafer 4020* (NY, LECTOTYPE); moist woods, Navas to Camp Buena Vista, alt. 650 m., *Shafer 4453* (NY, US); Minas de Iberia ad Taco Bay, alt. c. 800 m., *Ekman 3833, 3848* (S).

Evidently the commonest and most widespread of the three species of the subsection, *P. incrustatus* is morphologically the most specialized, at least with respect to its smaller leaves and androecium of fewer stamens. Although occasional large-leaved forms, such as *Ekman 3848*, simulate *P. williamioides*, the ensemble of characters of *P. incrustatus* is distinctive. In addition to its smaller leaves and fewer stamens, it also differs from *P. williamioides* in its persistent stipules and somewhat larger number of leaves per branchlet.

Although its small, roundish, coriaceous leaves suggest an affinity of *P. incrustatus* with the species of sect. *Orbicularia*, it does not appear likely that *P. incrustatus* is the progenitor of that group. Rather, it seems that the species of subsect. *Incrustati* represent a more or less parallel line of development with the representatives of *Orbicularia*.

Subsect. 16c. **Mirifici**, subsect. nov.[21]

Stems and branchlets smooth but with conspicuous lenticels; leaves of branchlets opposite, coriaceous (heavily sclerified within); stamens 5; styles obsolete, the greatly dilated stigmas (style-tips) forming a cap which covers most of the ovary.

TYPE SPECIES: *Phyllanthus mirificus* Webster.

The single very distinctive species of this monotypic taxon, only recently discovered in eastern Cuba, is unique among the New World species of *Phyllanthus* in its opposite leaves (on the branchlets) and hypertrophied stigmas. Although its leaf arrangement and androecium suggest certain Old World taxa, its areolate pollen grains, leaf structure, and aspect provide an incontestable basis for placing it in sect. *Williamia*. Its affinity with sect. *Incrustati* is evident from even superficial comparison, but its many distinctive characters amply justify the erection of a special subsect. *Mirifici*.

54. **Phyllanthus mirificus** Webster, Contr. Gray Herb. 176: 58. 1955. (PLATE XXVI, *figs.* A–C).

Definitely woody, presumably a shrub; branches slender, terete, not over 3 or 4 mm. thick (toward the ends), smooth, greyish- or reddish-brown, with conspicuous elliptic to linear lenticels. Cataphylls blackish and indurate but soon deciduous: stipules triangular-lanceolate, 2.3–3 mm. long, 1–1.5 mm. broad, acuminate, entire, carinate on the back; blade linear-lanceolate, c. 2 mm. long. Deciduous branchlets 8–13.5 cm. long, 1.5–2 mm. thick (those on lateral axes only 1 mm. thick), terete, smooth, brownish, becoming lenticellate proximally or throughout, with c. 6–8 (–11) pairs of leaves; first internode 6–20 mm. long, median internodes 3–20 mm. long. Leaves of branchlets all opposite (one node very slightly higher than its neighbor): stipules blackish and indurate but mostly soon deciduous, triangular-lanceolate, 2.2–3 mm. long, 0.6–0.9 mm. broad, acuminate, entire. Petioles 1.8–3 mm. long, brownish, plane and grooved down the middle adaxially, convex and corrugate-rugulose abaxially. Leaf-blades rigidly coriaceous, elliptic or ovate to suborbicular, 1.5–2.8 cm. long, 1.3–2.1 cm. broad, emarginate at the apex (the small short-conical dark brown apiculum of the juvenile leaf represented by a scar, or apparently absent), obtuse or rounded to subcordate at the base; above olivaceous or brownish, the midrib conspicuous, pale, plane or slightly sunken, the laterals obscured by the close-meshed slightly raised reticulum of tertiary veinlets; beneath more or less greyish-pruinose, the midrib nearly plane, the laterals (c. 5 or 6 on a side) and veinlets anastomosing in a subprominent reticulum; margins sharply differentiated, thin and acute, plane or reflexed (but not revolute).

[21] Subsect. **Mirifici**, subsect. nov. Ramis ramulisve lenticellatis; foliis ramulorum oppositis, coriaceis; staminibus 5; stigmatibus dilatatis, calyptratis. — Species typica *Phyllanthus mirificus* Webster.

Monoecious; flowers in axillary bisexual cymules, each with a solitary female and mostly 2 or 3 male flowers; bracteoles ovate, blackish and indurate, persistent.

Male flower: pedicel slender, c. 1–1.2 mm. long. Calyx reddish when dried; calyx-lobes 5, chartaceous, obovate, c. 1.5 mm. long, 0.9–1.3 mm. broad, rounded at the tip, entire, the midrib apparently unbranched. Disk-segments 5, ellipsoid, somewhat thickened, entire, c. 0.25–0.3 mm. across. Stamens 5; filaments connate into a column c. 0.5–0.8 mm. high, unequal in length (two anthers inserted lower than the other three); anthers subsessile, ascending or vertical, blunt, 0.3–0.4 mm. long, 0.4–0.45 mm. broad; anther-sacs divergent, dehiscing vertically, the slits not confluent; pollen grains 16–18 μ in diameter, areoles polybrochate, c. 6 μ across, c. 5–7 per amb.

Female flower: pedicel (at anthesis) 1.5–2.5 mm. long, subterete, enlarged and massive above. Calyx reddish when dried; calyx-lobes 6, subequal, biseriate, the outer broadly ovate, the inner broadly obovate, c. 1.5–1.8 mm. long, 1.1–1.4 mm. broad, entire, the veins obscure. Disk rather massive, bluntly angled, plane, the margins entire. Ovary subglobose, sessile, almost completely covered by the lower margins of the three dilated stigmas (style-ends) which are reflexed and appressed to form a close-fitting calyptra; stigmas with auricles connivent into a blunt beak at the top, the lateral margins entire, the distal margins crenulate-notched, 0.9–1.1 mm. long, 0.9–1 mm. broad across the distal edge.

Fruit and seeds unknown.

TYPE: Cuba, *León et al. 22613.*

DISTRIBUTION: scrublands and pinelands, northeastern Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Charrascal del Coco, south of Moa, July 1945, *León, Clemente, & Alain 22613* (MICH, HOLOTYPE; LS, ISOTYPE); charrascos y pinares, Sierra de Moa, alt. c. 750 m., 25 July 1953, *Alain 3380* (GH); pineland barrens, Charrascos de Peña Prieta, Toa, alt. 600 m., 30 Dec. 1953, *Alain 3616* (GH; sterile).

This extraordinary species, which remained undetected up until recent times, now appears to be as widely distributed in the Sagua-Baracoa range as some of the other specialized members of sect. *Williamia*. Its opposite branchlet-leaves and calyptriform stigmas at once set it apart from all of its West Indian congeners, and its androecium of 5 stamens in two unequal sets appears very similar to that in certain Old World species of subg. *Kirganelia*. Nevertheless, its phyllanthoid branching and areolate pollen grains show that it belongs in subg. *Xylophylla*, and both foliar and floral characters attest its affinity with the species of sect. *Williamia*. However, no one species of the section appears particularly close to *P. mirificus*, although *P. excisus* has a similar aspect (the type collection was, in fact, determined as that species), while *P. williamioides* has similar androecia and short-pedicellate flowers. In some ways, *P. mirificus* is

intermediate between subsects. *Discolores* and *Incrustati*; this is especially true of its development of copious lenticels, which presents a condition transitional between the smooth stems of subsect. *Discolores* and the scurfy axes of subsect. *Incrustati*. Because of this intermediary position and of its very divergent features, *P. mirificus* seems best assigned to a special subsection of its own.

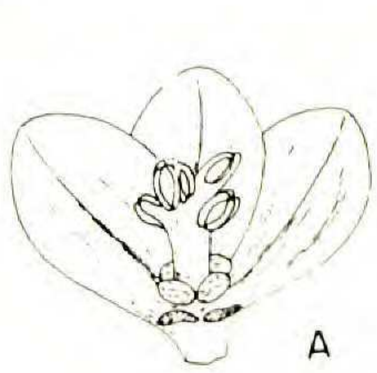
Sect. 17. **Thamnocharis** Webster, Contr. Gray Herb. 176: 59. 1955.

Shrubs with phyllanthoid branching; cataphylls large, indurate; leaves coriaceous, stipules caducous. Monoecious; cymules bisexual, the flowers appearing with the expanding leaves. Male flower: calyx-lobes 4–6; disk-segments 4–6; stamens 2–6 (–8), filaments united (apparently free in *P. comptus*), anthers dehiscing vertically; pollen grains areolate. Female flower: calyx-lobes 4–6, coriaceous; disk entire, angled; styles free or connate, bifid, the style-branches narrowed to acute tips. Capsule subglobose, dry, not veiny; seeds smooth or rugulose.

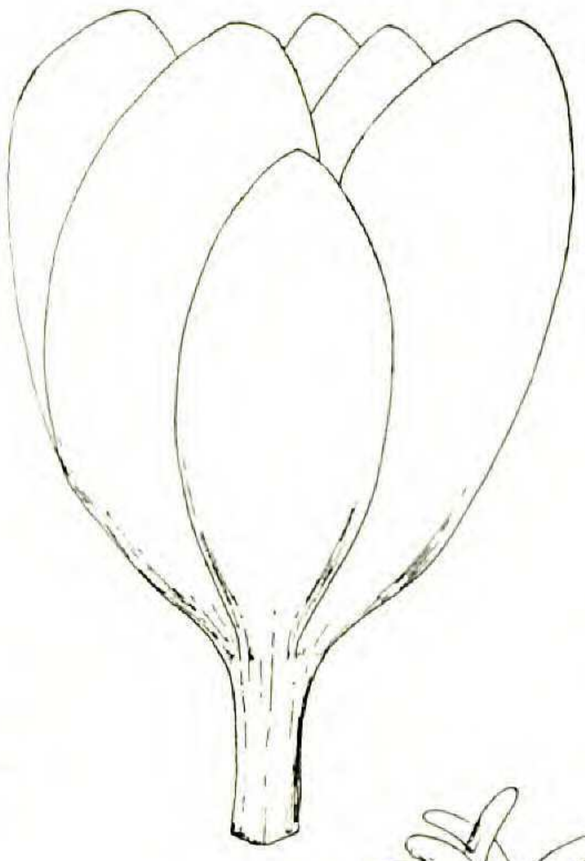
TYPE SPECIES: *Phyllanthus cinctus* Urb.

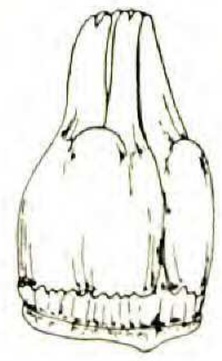
The relationships and nomenclature of this Cuban section and its three constituent species were discussed at some length in the original place of publication (op. cit. pp. 59–62). However, subsequent investigation has shown (on the basis of the presumed hybridization between *P. discolor* and *P. comptus*) that there must be a fairly close affinity between sects. *Williamia* and *Thamnocharis*; consequently, the position of the latter in the linear arrangement of sections has been altered. Furthermore, it is now clear that sect. *Thamnocharis* need not be compared with the Asiatic sect. *Eriococcodes*, for the latter definitely belongs in subg. *Eriococcus*, and its floral similarities are simply due to parallel evolution. Despite the dissimilarity (in gross appearance and in floral details) between *P. cinctus* and *P. discolor*, a significant affinity between subsect. *Discolores* (of sect. *Williamia*) and sect. *Thamnocharis* appears highly probable.

Before male flowers of *P. comptus* and before its hybridization with *P. discolor* were known, sect. *Thamnocharis* was thought to be related to sect. *Epistylium*. The Jamaican species of that section resemble the Cuban species of sect. *Thamnocharis* in their palm-like habit, reduced androecium, and similarly veined leaves. It may yet be possible to show that sect. *Epistylium* is closely related to the Cuban plants, but since its representatives (*P. cauliflorus* and *P. cladanthus*) differ in having persistent stipules, horizontally dehiscing anthers, and dilated lacerate styles, they are placed at some distance in the present linear arrangement. Even more similar to sect. *Thamnocharis*, at least superficially, is the monotypic sect. *Glyptothamnus* which closely mimics *P. cinctus*; but that group appears to be much more closely allied to sect. *Epistylium* in its technical characters. These rather puzzling suggestions of reticulate relationships indicate that the phylogeny of the groups in question can by no means be considered finally settled.



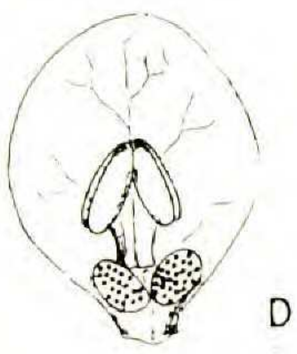
A



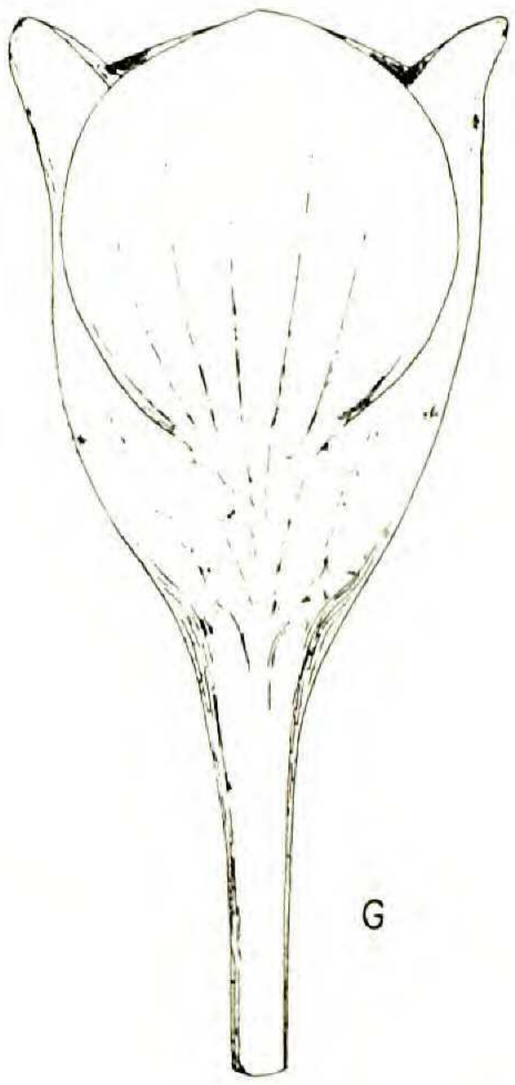


C

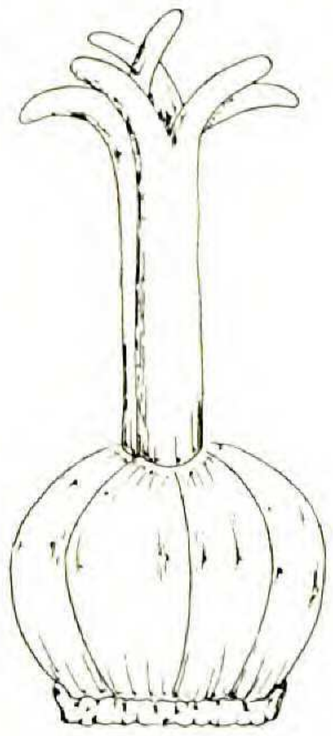
0 —— 1
mm.



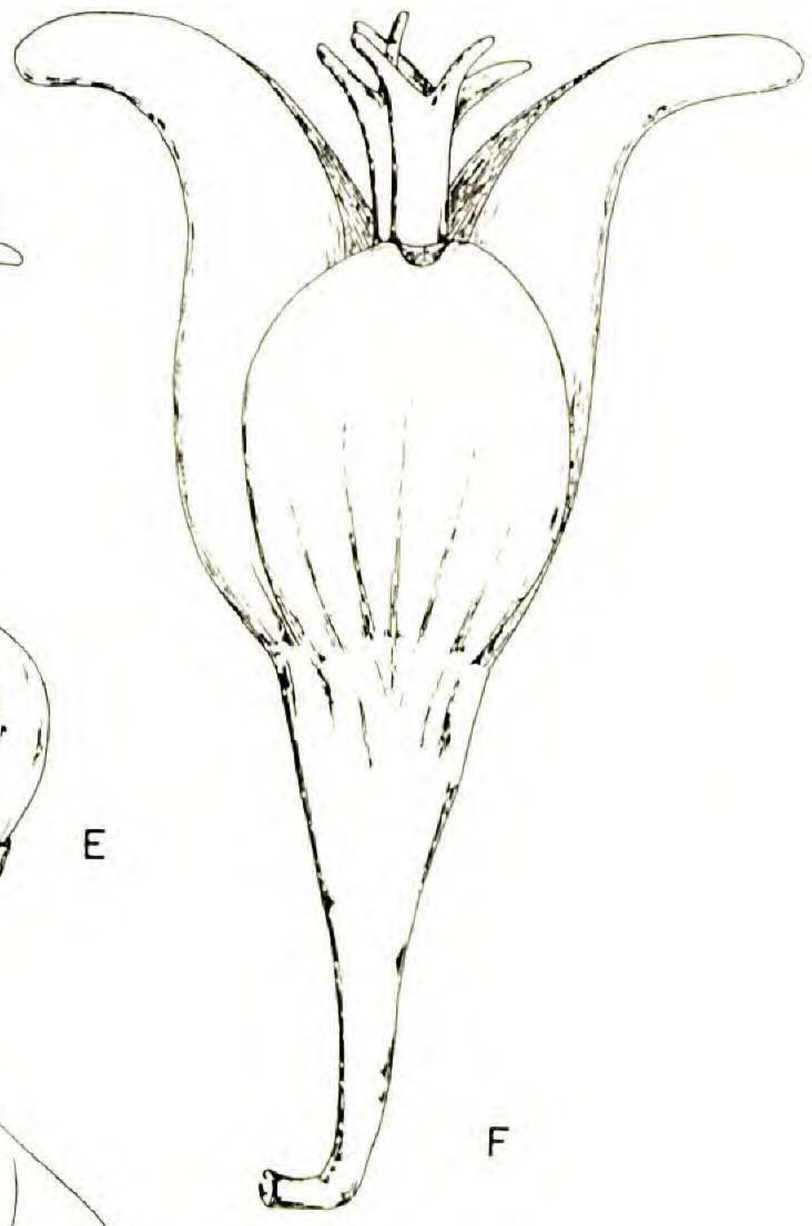
D



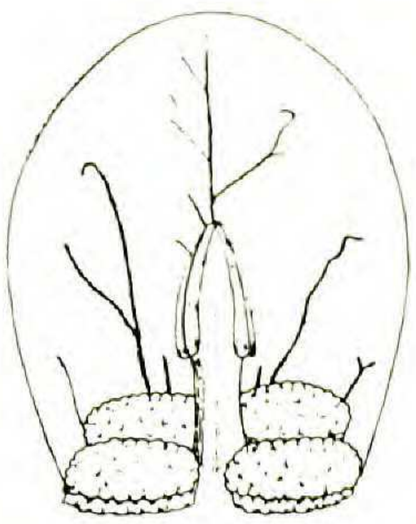
G

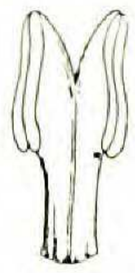


E

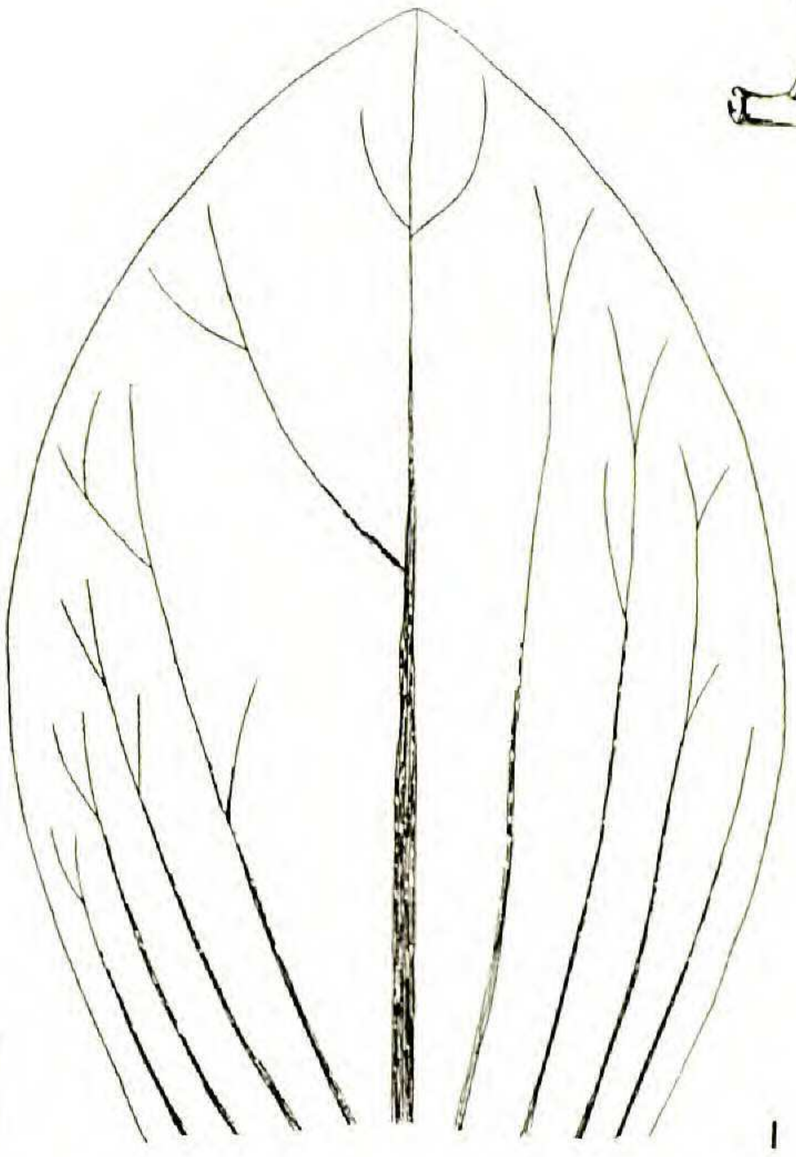


F

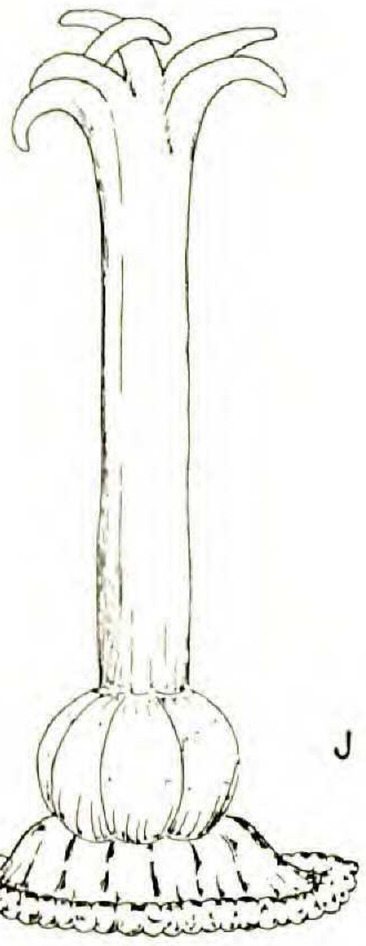




H



I



J

WEBSTER, WEST INDIAN PHYLLANTHUS

KEY TO THE SPECIES

1. Calyx-lobes and stamens 5 or 6; styles free; pedicel of female flower 10–14 mm. long; seeds vermiculately marked, 4.5 mm. long or more; cataphyllary stipules ribless, less than 1 cm. long. ..... 55. *P. comptus*
1. Calyx-lobes 4; stamens 2; styles united into a column; pedicel of female flower not over 6 mm. long; seeds smooth, not over 4 mm. long; cataphyllary stipules longitudinally ribbed, 1 cm. long or more.
   2. Male calyx-lobes c. 2 mm. long, with mostly 1–3 nerves from the base; anthers triangular, 0.5–0.8 mm. long; female calyx-lobes reflexed at the tips, the inner (longer) c. 3–5 (–6) mm. long; female disk tenuous, rim-like, c. 2 mm. across. ..... 56. *P. cinctus*
   2. Male calyx-lobes c. 3–3.5 mm. long, with mostly 5–7 nerves from the base; anthers lanceolate, 0.9–1.2 mm. long; female calyx-lobes not reflexed at the tips, the inner (longer) becoming 6–8 mm. long; female disk very massive, forming a mound 3–4 mm. broad and 0.5–1 mm. high, its foveolate rim depressed. ..... 57. *P. ekmanii*

55. **Phyllanthus comptus** Webster, Contr. Gray Herb. **176**: 61. 1955.

Glabrous shrub; branches terete, smooth, pale brown becoming greyish, c. 3–4 mm. thick. Cataphylls massive and coriaceous but deciduous: stipules triangular-lanceolate, acuminate, c. 6–7.5 mm. long, 2–3 mm. broad, obliquely truncate at the base, brownish with blackened indurate tips; blade narrower. Deciduous branchlets (5.5–) 7–14 cm. long, 1–1.5 mm. thick, stramineous or pale reddish brown, smooth, subterete (somewhat flattened proximally), with only 5–7 nodes; first internode (15–) 20–30 mm. long, median internodes c. 15–30 mm. long. Leaves: stipules caducous, ovate-lanceolate, 5–6 mm. long, 2.7–3 mm. broad, acuminate, more or less denticulate along the margin, brownish, scarious-chartaceous with more or less indurate darkish tips. Petioles plane adaxially, convex abaxially, smooth, stramineous or reddish brown, 2.5–4 mm. long. Leaf-blade coriaceous, ovate or elliptic, c. (2.5–) 3–5.5 cm. long, (1.2–) 1.5–3 cm. broad, obtuse and minutely apiculate at the tip, obtuse or rounded at the base; above sublucid, olivaceous, the midrib and chief laterals slightly raised; beneath paler, the midrib and main laterals (4 or 5 on a side) slightly raised, forming a subprominent reticulum, veinlets obscure; margins cartilaginous-thickened, light brownish, more or less reflexed.

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules usually bisexual, of 1 female and several (c. 5–8) male flowers.

PLATE XXVI. FLOWERS OF SECT. *Williamia*, SUBSECT. *Mirifici*, AND OF SECT. *Thamnocharis*.

FIGS. A–C. Male flower, female calyx, and gynoecium of *Phyllanthus mirificus* Webster (*Alain 3380* [GH]). FIGS. D–F. Male flower, female flower, and gynoecium of *Phyllanthus cinctus* Urb. (*Jervis 3355* [GH]). FIGS. G–J. Male flower, androecium, female calyx-lobe, and gynoecium of *Phyllanthus ekmanii* Webster (*Jervis 3037* [GH]).

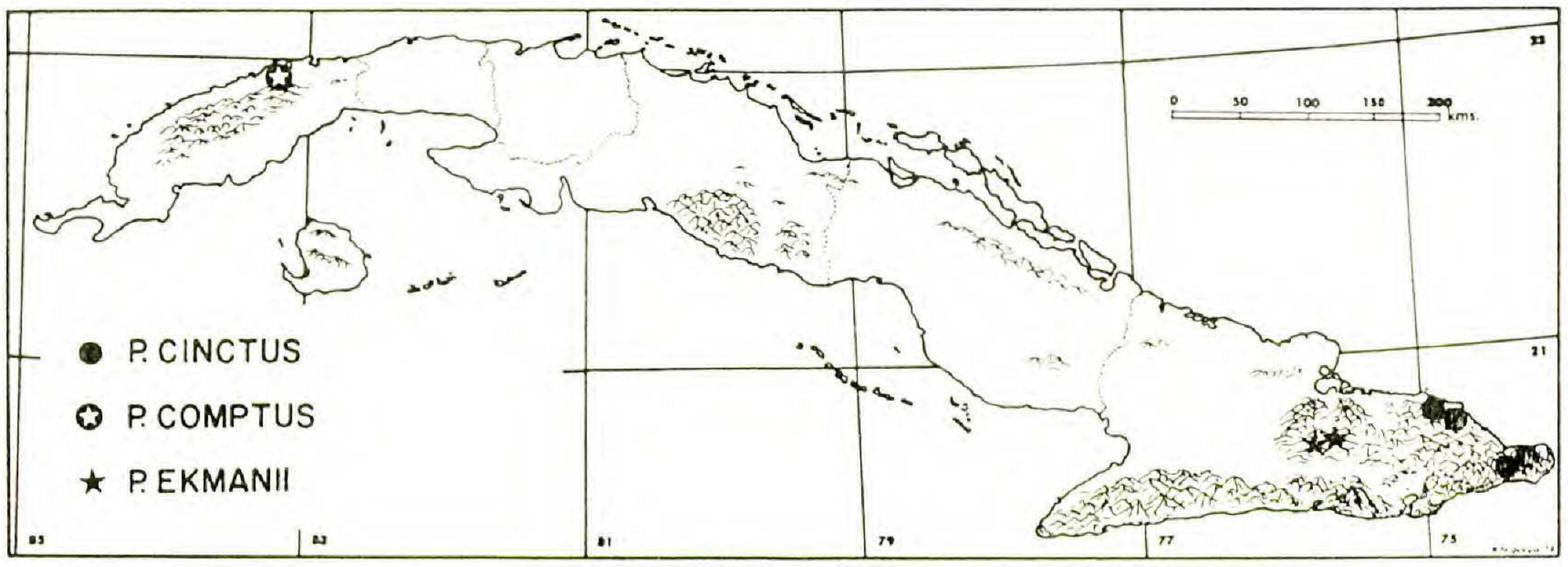
Male flower (described from immature buds): pedicel up to c. 2.5 or 3 mm. long. Calyx-lobes 6 (rarely 5), greenish, nervation obscure; disk-segments 6 (rarely 5), flattened, foveolate; stamens (4–) 5 or 6 (–8), filaments shorter than anthers and apparently not united (but staminal column perhaps not yet developed); anthers reniform, c. 0.4–0.5 mm. broad; anther-sacs divergent, dehiscing more or less vertically, the slits apically confluent.

Female flower: pedicel slender, subterete below, gradually dilated and obtusely angled above the middle, 10–14 mm. long. Calyx-lobes 6 (rarely 5), unequal, spathulate, rounded and entire at the tip, in flower 2.5–4 mm. long and 1.2–1.7 mm. broad, in fruit 3.3–4.2 mm. long, c. 1.7 mm. broad, the nerves obscure. Disk flat, 6-angled, becoming dark brown, not conspicuous. Ovary reddish brown, sulcate, emarginate at the top; styles free except at the very base, ascending, c. 1.5 mm. high, bifid; style-branches divergent, recurving, terete, narrowed to the tips.

Capsule-valves c. 7–7.5 mm. long, reddish brown, the veins obscure. Columella 3.8–4 mm. long. Seeds trigonous, asymmetric, carinate or somewhat irregular on the back, (4.5–) 4.8–5.1 mm. long, (2.5–) 3 mm. tangentially (across the back), dark brown (to the naked eye), with a vermiculate pattern of brownish-black raised lines on a light brown background; hilum submedian, c. 0.4–0.5 mm. across, the raphe conspicuous.

TYPE: Cuba, *Acuña 18222*.

DISTRIBUTION: endemic to the Cajálbana region, Pinar del Río province, Cuba (MAP XXIV).



MAP XXIV. Distribution of sect. *Thamnocharis* in Cuba.

CUBA. PINAR DEL RÍO: en arroyos, La Cajálbana, La Mulata, 28 Sept. 1952, *Acuña 18222* (SV, HOLOTYPE; fruiting); banks of a rivulet, cuabales, east of Loma Cajálbana, La Palma, Oct. 1952, *Acuña* (LS, MICH); La Cajálbana, junto a cañada, Camino de Sagua, 12 Mar. 1954, *Acuña & Schubert 19120* (GH, PARATYPE; male and female flowers).

This recently described species, which would still remain unknown were it not for the efforts of Ing. Julian Acuña, needs further study. Good material of the male flowers is sparse or lacking in most specimens of this and the other two species of sect. *Thamnocharis*, because the flowers appear

with the developing leaves and the male ones are soon deciduous. The androecium of *P. comptus* is of especial interest because of the apparently free filaments and the variable number of stamens. A count of 25 flowers yielded the following distribution (the first figure being the stamen number): 4 — 3, 5 — 9, 6 — 11, 7 — 1, 8 — 1. This range of variation nicely bridges the gap between the androecium of *P. discolor*, with 9–14 stamens, and the other two species of sect. *Thamnocharis*, with only 2. The presumption that *P. comptus* represents a phylogenetically important connecting link is thus strengthened.

Although there appears to be no serious doubt regarding the kinship of *P. comptus* with *P. cinctus* and *P. ekmanii*, the differences between the Pinar del Río and Oriente plants are so profound that their separation must be ancient; they could be placed in different subsections if there were any point in subdividing so small a section as *Thamnocharis*. The recognition of the hybridization between *P. comptus* and *P. discolor* (discussed in detail under the latter) has further complicated the picture. Although these two species obviously retain some degree of genetic compatibility, the cataphylls, leaves, styles, and seeds of *P. comptus* are so different from those of *P. discolor* that each species must represent the end-product of a long-separate evolutionary line. In common with several other species endemic to the Cajálbana area, *P. comptus* bears the earmarks of a relict species the nearest relatives of which have long since disappeared.

56. **Phyllanthus cinctus** Urb. Symb. Ant. **9**: 191–192. 1924; emend. Webster, Contr. Gray Herb. **176**: 60. 1955.

(PLATE XXVI, *figs.* D–F).

Conami (?) ovalifolia Britton, Mem. Torr. Bot. Club **16**: 73–74. 1920; non *Phyllanthus ovalifolius* Forsk., 1775.
Phyllanthus brittonii Alain, Contr. Mus. La Salle **11**: 1. 1952.

Subshrub or shrub 0.15–1 m. high, with the habit of a miniature tree, the primary stem unbranched, greyish, furrowed, c. 4–8 mm. thick. Lower leaves (missing on many specimens) with petioles c. 5–7 mm. long, leaf-blades obovate or spathulate, 4–6.5 cm. long; upper leaves reduced to cataphylls: stipules triangular-lanceolate (somewhat falcate), acuminate, 10–17 mm. long, 4–5 mm. broad (on vigorous shoots; sometimes as small as 7 mm. long and 3.5 mm. broad on weak axes), obliquely truncate at the base, conspicuously longitudinally corrugate-ribbed, dull reddish brown, somewhat blackish and glandular at the base, sometimes densely hirtello-scabridulous at the base or throughout, scarious-indurate; blade acicular, 7.5–9 mm. long. Deciduous branchlets erect to spreading, (10–) 15–23 cm. long, 2.5–3 mm. broad, olivaceous, smooth or pustulate-scabridulous, distinctly flattened, with c. (4–) 8–15 leaves; first internode (15–) 20–50 (–65) mm. long, median internodes (10–) 15–25 (–40) mm. long. Leaves: stipules caducous (represented in most specimens only by small scars), broadly lanceolate, c. 3.5–4 mm. long, acuminate, entire or obscurely denticulate, brownish, scarious. Petioles subterete (somewhat flattened adax-

ially), rugulose or sometimes scabridulous, 2.5–5 mm. long. Leaf-blades coriaceous, oblong-elliptic, tending to be slightly obovate, (3–) 4–8 cm. long, (1.5–) 2–3.5 (–4.5) cm. broad, obtuse or rounded and with a minute blackish apiculum (sometimes obsolete) at the tip, acute to obtuse at the base; above sublucid or dully olivaceous, minutely foveolate, the midrib plane or slightly raised, the lateral and tertiary veins anastomosing in a somewhat prominent reticulum; beneath paler, the midrib prominently raised, the laterals (mostly 6–10 on a side) and veinlets forming a prominent reticulum; margins with a reflexed thickened marginal rim (which is colored as the rest of the undersurface).

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules bisexual, of 1 or 2 (rarely 3) female and c. 10–12 male flowers.

Male flower: pedicel slender, 3–5 mm. long. Calyx purplish or dark red; calyx-lobes 4, chartaceous, biseriate, the outer broadly ovate or oblong, the inner obovate or suborbicular, 1.9–2.1 mm. long, 1.4–2 mm. broad, rounded and entire at the tip, mostly 3-nerved, the irregular veins dark and conspicuous. Disk-segments 4, irregularly cubical or subglobose, foveolate-pitted, 0.4–0.6 mm. across. Stamens 2; filaments completely connate into a rather slender terete column usually 0.6–0.9 mm. high and 0.2–0.25 mm. thick; anthers erect, sessile atop the column, discrete or fused back-to-back below, triangular-ovate, (0.5–) 0.6–0.8 mm. long, 0.4–0.5 mm. broad; anther-sacs subparallel, dehiscing vertically, the slits not confluent; pollen grains c. 20–24 μ in diameter, areoles oligobrochate or transitional to polybrochate, c. 12–15 per amb, 4–6 μ across.

Female flower: pedicel terete and slender at the very base but abruptly dilated above, not angled, 4–5 mm. long. Calyx purplish or dark red; calyx-lobes 4, coriaceous, biseriate, subequal or unequal, at anthesis more or less spreading with the tips reflexed, elliptic to broadly ovate-oblong, the larger lobes c. 3–5 (–6) mm. long and 2–4 (–5) mm. broad, rounded or obtuse at the tip, triplinerved but the laterals much less conspicuous than in the male calyx, mesophyll densely crystalliferous. Disk squarish, the 4 coalesced segments forming a shallow undulate-crenulate, foveolate-pitted cup c. 2 mm. across. Ovary reddish brown, sulcate, the tips of the carpels slightly projecting above the insertion of the styles; styles erect, 2.3–3.5 mm. high, connate into a comparatively slender column 1.7–2.4 mm. high and 0.4–0.55 mm. thick; stylar branches divergent, recurving, terete and narrowed to subacute tips.

Capsule obtusely angled, c. 5.5–6 mm. in diameter, smooth, reddish-brown, not veiny. Columella 2.5–3 mm. long. Seeds trigonous, symmetric, 3.7–4 mm. long, 2.4–2.8 mm. radially and tangentially, reddish brown, smooth (minutely colliculose); hilum subterminal, elliptic, c. 0.5 mm. long.

Collected flowering Feb.–Apr., Aug.; fruiting Feb.–Mar., July.

TYPE: Cuba, *Shafer 8446*.

DISTRIBUTION: serpentine areas, usually in pinelands, eastern Oriente province, Cuba (MAP XXIV).

CUBA. ORIENTE: Cananova, sur le charrascal serpentineux du Cerro de Miraflores, 16–23 Apr. 1943, *Marie-Victorin, Clement, & Alain 21634* (MT); vicinity of Moa, Arroyo Moa, 10 Apr. 1945, *Acuña 12479* (SV, US); Moa, pinares, summer 1939, *Mrs. Bucher 61* (NY, SV); Moa, río de la scierie, 16–23 Apr. 1943, *Marie-Victorin, Clement, & Alain 21635* (MT); Moa, 29 Aug. 1917, *Roig 1545* (NY, SV); wet pinelands near Punta Gorda, 14 July 1947, *León & Clemente 23057* (MICH); rich woods, alluvial valley of Río Yamaniguey, 27 Feb. to 1 Mar. 1910, *Shafer 4228* (NY, US), *4274* (F, NY); between Yamurí Arriba and Bermejal, Feb. 1911, *Shafer 8446* (NY, LECTOTYPE); Cuchillas de Baracoa, c. 1 mi. north of Río Yumurí, pinelands, alt. c. 2000 ft., 18 Mar. 1954, *Jervis 3355* (GH).

Of the three species of sect. *Thamnocharis, P. cinctus* is the commonest and most widespread, occupying relatively mesophytic riparian habitats as well as drier pinelands or scrub. It correspondingly is the most variable of the three species, and *Jervis 3355* is particularly divergent due to its large female calyx (the longer lobes being 6 by 5 mm. instead of 3–5 by 2–4 mm.) and smaller leaves with only 5–7 lateral veins. In these respects it partially closes the morphological gap between *P. cinctus* and *P. ekmanii* and provides additional support for the possible alternative course of grouping these plants as two subspecies of a single species. Nevertheless, the gap — although narrowed — remains, and until further knowledge of the range of variation can be obtained, the present arrangement appears to be the best.

Also occurring in the Moa region within the range of *P. cinctus* is the narrowly endemic *P. chryseus* (sect. *Glyptothamnus*), which is strikingly similar in its habit, tetramerous calyx and androecium of two stamens. However, it differs in so many important respects (e.g., persistent stipules, unisexual inflorescence, annular male disk, lacerate styles) that the similarity to *P. cinctus* would seem to be ascribable to convergent development rather than to a close affinity.

57. **Phyllanthus ekmanii** Webster, Contr. Gray Herb. **176**: 60. 1955. (PLATE XXVI, *figs.* G–J; PLATE XXVII, *fig.* B).

Phyllanthus cinctus Urb. Symb. Ant. **9**: 191–192. 1924 (as to description, not as to type).

Subshrub or treelet, with the habit of *P. cinctus,* 0.3–1 m. high. Lower leaves of main axis (missing on many specimens) with petioles 5–7 mm. long, leaf-blades obovate or broadly elliptic, 3.5–6.5 cm. long and 2–4 cm. broad; upper leaves reduced to cataphylls: stipules triangular-lanceolate, acuminate, 10–17 mm. long, 4–5 mm. broad (on vigorous shoots; sometimes as small as 7 mm. long and 3.5 mm. broad), truncate at the base, conspicuously longitudinally corrugate-ribbed, dull reddish brown, scarious-indurate; blade acicular. Deciduous branchlets erect to spreading, (8–) 10–23 cm. long, 2.5–3 mm. broad, olivaceous, smooth or pustulate-scabridulous, distinctly flattened, with c. 7–15 leaves; first internode 15–45 mm. long, median internodes 10–25 mm. long. Leaves: stipules cadu-

cous (represented in most specimens only by small scars), lanceolate, c. 1.5–2 mm. long, acuminate, obscurely denticulate, brownish, scarious. Petioles somewhat flattened adaxially, rugulose, sometimes scabridulous, (2–) 2.5–4 mm. long. Leaf-blades stiffly coriaceous, elliptic to slightly ovate, (2.5–) 3–5 (–6) cm. long, 1.3–3 (–3.5) cm. broad, obtusely rounded or emarginate at the tip (the minute blackish apiculum nearly or quite obsolete), cuneate to obtuse or rounded at the base; above sublucid, minutely foveolate, the midrib plane or slightly raised, the lateral and tertiary veins anastomosing in a prominent somewhat raised reticulum; beneath paler, the midrib prominently raised, the lateral (c. 4–6 on a side) and tertiary veins forming a reticulum more prominent than that above; margins with a reflexed thickened brownish or somewhat orange marginal rim.

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules bisexual, of 1 or 2 female and c. 2–5 male flowers.

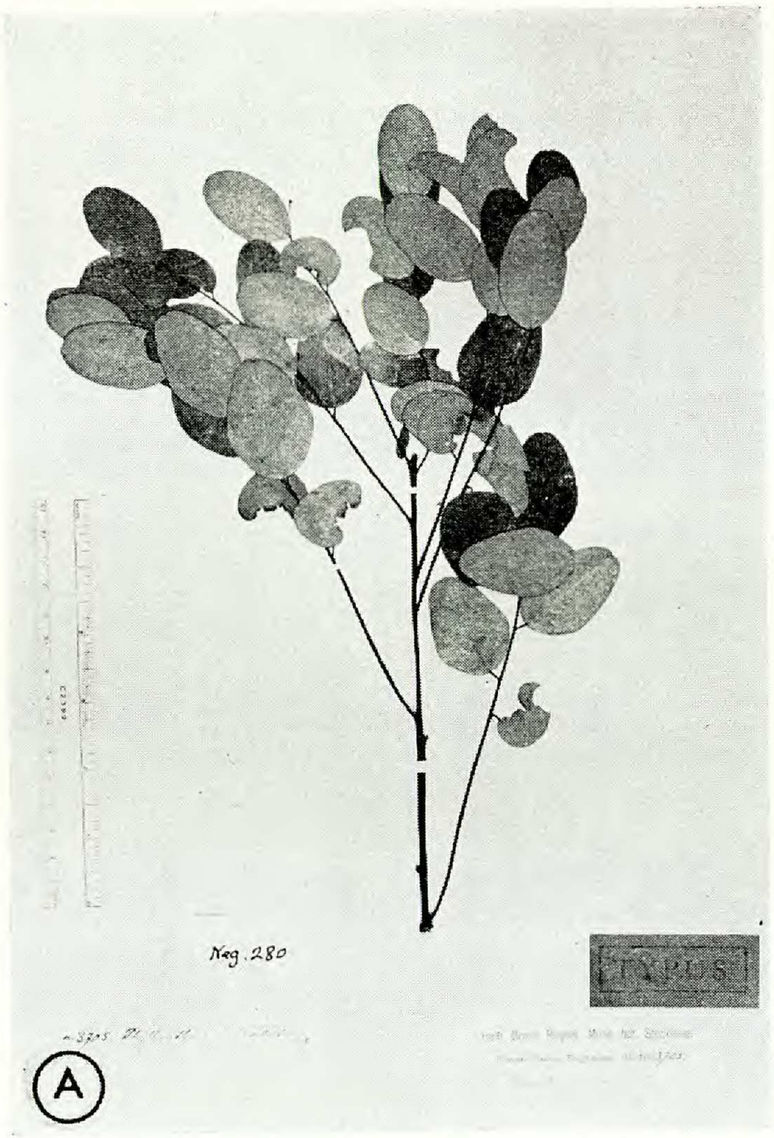
Male flower: pedicel slender, becoming 4–9 mm. long, abruptly dilated and fleshy above. Calyx dark reddish (rarely creamy-white?); calyx-lobes 4, chartaceous, biseriate, suborbicular, 3–3.7 mm. long, 2.3–2.7 (–3) mm. broad, rounded and entire at the tip, ordinarily with 5–7 nerves from the base but these not very conspicuous. Disk-segments 4, subrectangular, more or less flattened, rugulose, c. 0.7–1.1 mm. across. Stamens 2; filaments completely connate into a stout column c. 0.5–0.8 mm. high and 0.6 mm. thick; anthers erect, sessile atop the column, fused back-to-back from ⅓ to all their lengths, narrowly triangular-lanceolate, c. 1–1.2 mm. long, 0.5–0.7 mm. broad; anther-sacs slightly divergent, dehiscing vertically, the slits not confluent; pollen grains c. 24–28 μ in diameter, areoles oligobrochate, mostly 15–18 per amb, c. 4–6 μ across.

Female flower: pedicel terete and slender at the base but abruptly dilated above, not angled, 2.5–5 (–6) mm. long. Calyx dark reddish (rarely creamy-white?); calyx-lobes 4, coriaceous, biseriate, subequal, broadly ovate or elliptic (the outer strongly convex, the inner conduplicate), erect (the tips not reflexed), the larger lobes 6–8 mm. long and 3–5 mm. broad, rounded at the tip, with c. 6 or 7 subparallel conspicuously reticulate-ramifying nerves, mesophyll densely crystalliferous. Disk squarish, very massive, forming below the ovary a mound-like pedestal c. 0.5–1 mm. high and 3–4 mm. broad, the foveolate rim depressed.

Ovary reddish brown, strongly sulcate; styles erect, 3–5 mm. high, connate into a column (2.1–) 2.5–4 mm. high and c. 0.4 mm. thick (somewhat dilated upwards); stylar branches divergent, slender, recurving, terete and narrowed to subacute tips.

Capsule valves c. 5 mm. long, reddish brown, smooth, not veiny. Columella nearly 3 mm. long. Seeds trigonous, nearly symmetric, 3.3–3.4 mm. long, 2–2.2 mm. radially, 2.2–2.5 mm. tangentially, reddish brown, smooth (minutely colliculose); hilum subterminal, ovoid or elliptic, c. 0.5 mm. long.

Collected flowering Feb., Apr., Aug.; fruiting May, June, July.



GROWTH FORM IN SECTS. *Williamia* AND *Thamnocharis*. FIG. A. *Phyllanthus microdictyus* Urb. (*Ekman 3705* [S, HOLOTYPE]). FIG. B. *Phyllanthus ekmanii* Webster (*Ekman 2523* [S, HOLOTYPE]); note the unreduced leaves on the lower part of the main axis.

TYPE: Cuba, *Ekman 2523*.

DISTRIBUTION: restricted to serpentine areas of the Sierra de Nipe, Oriente province, Cuba (MAP XXIV).

CUBA. ORIENTE, SIERRA DE NIPE: Cayo del Rey, Pinar Colorado, 16 Apr. 1940, *Carabia 3587* (MICH, NY); Río Piloto, locis rupestribus, alt. 750 m., 18 Aug. 1914, 15 May 1915, *Ekman 2523* (S, HOLOTYPE; NY, ISOTYPE), *5704* (S); charrascales, Río Piloto, 10 June 1915, 27 Apr. 1919, *Ekman 6026, 19166* (S); charrascales, ad viam Bio, 27 Apr. 1919, *Ekman 9583* (S); exposed ridge, Pico Estrella, 18 Feb. 1954, *Jervis 3037, 3065* (GH).

This species endemic to the Sierra de Nipe is so closely related to *P. cinctus* that Urban's confusion (in associating specimens of the former with the name of the latter) is understandable. Although some of the distinctions between the two taxa are not quite absolute and may even further break down upon study of additional collections, there are so many points of difference that it seems preferable to rank them as closely related allopatric species rather than as two subspecies of one variable species. The larger size of the male flower, at least, always distinguishes *P. ekmanii*; and its hypertrophied female disk, which somewhat recalls the gynophore of *P. microdictyus*, is very different from the unmodified disk of *P. cinctus*. In addition, the female calyx and styles of *P. ekmanii* appear to be definitely larger than those of *P. cinctus*, but the dimensions of these organs are subject to such variation after anthesis that on the basis of specimens at hand it is difficult to make comparable measurements. There are, furthermore, additional differences in the mean values of such characters as leaf-size and vein-number which lend support to the suppositon that *P. ekmanii* and *P. cinctus* are distinct species.

In contrast to *P. cinctus*, which ranges over much of the Sagua-Baracoa massif, *P. ekmanii* has a much more restricted range; it has thus far been collected only in the southern part of the Sierra de Nipe but not in the vicinity of Loma Mensura or Bandera. The only divergent specimen noticed was *Jervis 3037* which, according to the collector, had "creamy-white" rather than reddish flowers. Unfortunately no flowers were present on the single available specimen of this collection number; but since *Jervis 3065* from the same locality has typically reddish flowers, it would appear that the whitish-flowered form is only a trivial local variant.

(*To be concluded*)